PB81-159816

The Molluscan Shell
Biological Record of Environmental Change

Yale Univ.
New Haven, CT

Prepared for

Environmental Research Lab.
Narragansett, RI

Feb 81

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EPA 600/3-81-019
February 1981

PB81-159816

THE MOLLUSCAN SHELL: BIOLOGICAL RECORD OF ENVIRONMENTAL CHANGE

Edited by

D.C. Rhoads and R.A. Lutz

Department of Geology and Geophysics
Yale University
New Haven, Connecticut 06520

and

Ira C. Darling Center
University of Maine
Walpole, Maine 04573

Grant 804909

Project Officer

Gerald Pesch
Environmental Research Laboratory
South Ferry Road
Narragansett, Rhode Island 02882

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TECHNICAL REPORT DATA
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1. REPORT NO. EPA-600/3-81-019	2.	3. RECIPIENT'S ACCESSION NO. PB81 159816
4. TITLE AND SUBTITLE The Molluscan Shell: Biological Record of Environmental Change		5. REPORT DATE February 1981 Issuing Date. 6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S) D. C. Rhoads and R. A. Lutz		8. PERFORMING ORGANIZATION REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS Department of Geology and Geophysics, Yale University, New Haven, CT 06520 and Ira Darling Center, University of Maine, Walpole, ME 04573		10. PROGRAM ELEMENT NO. 1BA819 11. CONTRACT/GRANT NO. R804909
12. SPONSORING AGENCY NAME AND ADDRESS Environmental Research Laboratory, Narragansett South Ferry Road Narragansett, RI 02882		13. TYPE OF REPORT AND PERIOD COVERED Final 14. SPONSORING AGENCY CODE EPA/600/05

15. SUPPLEMENTARY NOTES
This project has been financed in part with federal funds from the Environmental Protection Agency.

16. ABSTRACT

This manual of molluscan shell growth has been prepared so that the pollution biologist confronted with after-the-fact monitoring problems can extract information about recruitment, growth, and mortality responses of molluscs to past and present changes in environmental quality. This information is stored within individual molluscan shells in the form of ontogenetic records fo growth and development: larval top shells, internal microgrowth increments, and changes in shell microstructures (Chapters 1-4). An example of how internal growth increments can be used in this way is given for Mercenaria mercenaria exposed to a power plant thermal plume (Chapter 3).

Environmental change is also manifested at the population level in the form of temporal or spatial changes in the structure of whole-shell size-frequency distirbutions of both living and dead assemblages. An example of this approach is given for two bivalve life assemblages, Nucula annulata and Mulinia lateralis from central Long Island Sound. Populations living on a dredge-spoil dump site show very different survivorship cuvres than those populations living on the unpolluted seafloor (Chapter 5).
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17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group
biological indicators, marine biology (water pollution efforts), marine resources, marine environments, shellfish, mollusca, monitoring	molluscan shell growth, molluscan populations, molluscan shell record, pollution, historical record	

18. DISTRIBUTION STATEMENT RELEASE TO PUBLIC	19. SECURITY CLASS *(This Report)* UNCLASSIFIED	21. NO. OF PAGES
	20. SECURITY CLASS *(This page)* UNCLASSIFIED	22. PRICE

EPA Form 2220-1 (9-73)

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FOREWORD

The Environmental Research Laboratory of the U.S. Environmental Protection Agency is located on the shore of Narragansett Bay, Rhode Island. In order to assure the protection of marine resources, the laboratory is charged with providing a scientifically sound basis for Agency decisions on the environmental safety of various uses of marine systems. To a great extent, this requires research on the tolerance of marine organisms and their life stages as well as of ecosystems to many forms of pollutant stress. In addition, a knowledge of pollutant transport and fate is needed.

This report presents a manual of techniques, derived from the paleoecologic literature, on methods of obtaining information about dynamic aspects of molluscan life history from shells. The manual includes a comprehensive bibliography and each technique is illustrated with examples from the literature. The text is written so that anyone with a basic knowledge of invertebrate biology, ecology, and introductory statistics can use the reference to solve field problems. As a matter of illustration, the techniques used in the manual have been applied to mollusc populations associated with the New Haven, Connecticut, dump site (mud on mud) and the Oyster Creek power plant site in New Jersey.

Tudor T. Davies
Director, ERLN

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ABSTRACT

The responses of benthic organisms to temporal and spatial changes in environmental quality cannot always be directly measured. For instance, one may wish to assess the effect of a storm, pollution event, change in salinity, temperature, sediment type, etc. on a species population after the change (or event) has taken place. In the absence of data about pre-disturbance rates of reproduction, recruitment, growth and mortality, the biologist must depend on an indirect or deductive approach. This kind of after-the-fact problem is common in paleoecology and is an increasingly important one in pollution biology.

This manual of molluscan shell growth has been prepared so that the pollution biologist, confronted with after-the-fact monitoring problems, can extract information about recruitment, growth, and mortality responses of molluscs to past and present changes in environmental quality. This information is stored within individual molluscan shells in the form of ontogenetic records of growth and development: larval top shells, internal microgrowth increments, and changes in shell microstructures (Chapters 1-4). An An example of how internal growth increments can be used in this way is given for *Mercenaria mercenaria* exposed to a power plant thermal plume (Chapter 3).

Environmental change is also manifested at the population level in the form of temporal or spatial changes in the structure of whole-shell size-frequency distributions of both living and death assemblages. An example of this approach is given for two bivalve life assemblages, *Nucula annulata* and *Mulinia lateralis* from central Long Island Sound. Populations living on a dredge-spoil dump site show very different survivorship curves than those populations living on the ambient seafloor (Chapter 5).

Appendices are included which provide practical information in preparing the molluscan shells for microscopical and ultrastructural study of ontogenetic growth patterns.

This report was submitted in fulfillment of contract No. R804-909-010 by Yale University under sponsorship of the U.S. Environmental Protection Agency. This report covers the period October 15, 1976 - October 14, 1978.

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ACKNOWLEDGMENTS

In 1975, we (DCR and RAL) had discussions with Eric Schneider, Director of EPA Water Quality Laboratory, Narragansett, Rhode Island about the potential of using shell growth analysis to monitor environmental change. These preliminary discussions subsequently resulted in our working with the EPA to explore the utility of using molluscan shell growth records in water pollution studies. We wish to thank Eric Schneider, Gerald Pesch, and Robert Payne of the Narragansett Laboratory for their early interest and support of our project.

A major task in assembling a multiauthored volume is the review of manuscripts. This has been less of a task than we originally thought because the following reviewers were very responsive to our requests for prompt, yet thoughtful and critical reviews: A. Clarke, J.R. Dodd, R. Fairbanks, R. Green, M. Kennish, J. Levinton, A.L. McAlester, C. MacClintock, E. McCoy, G. Pannella, S. Rachootin, R. Robertson, S. Stanley, R. Scheltema, F. Stehli, R. Strathmann, J.D. Taylor, C. Thayer, I. Thompson, D. Townsend, R.D. Turner, R. Vaisnys, and T.R. Waller.

Mr. Dwight Muschenheim assisted us with the many details of styling and proofreading of manuscripts. We also wish to thank our typists who saw us through several drafts of edited copy: Betsy Dabakis and Doreen Orciari of the Department of Geology and Geophysics, Yale University, and Susan Shiminski, Maxine Lane, Constance Williams, Stephanie Clifford, and Lois Lane of the Ira C. Darling Center, University of Maine. Supported by EPA grant R-804-909-010, and NOAA Sea Grants 04-6-158-44056, SGI-77-17, and 04-7-158-44034.

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INTRODUCTION

I. THE PERSPECTIVE OF THIS MANUAL

A wealth of information about past and present-day environments is contained within the shells of fossil and living molluscs. Information about an organism's dynamic environment is capable of being preserved as a structural, morphological, or chemical change in the shells of individuals. The demographic structure of a species population also contains much environmental information. Research into these relationships has, in the past, been largely for the purpose of reconstructing paleoenvironments. The implications of this approach for ecological work has recently interested many neontologists. The ecologist is frequently concerned with reconstructing environmental events after they have taken place. For instance, it may be desirable to assess the effects of major storms, salinity fluctuations, temperature changes, or pollution events on organisms after the event or change has taken place. In the absence of information about pre-disturbance rates of reproduction, recruitment, growth, and mortality, the ecologist, like the paleoecologist, is confronted with a problem of after-the-fact data acquisition. Shell growth records can address this kind of problem.

II. HOW ENVIRONMENTAL CHANGE IS RECORDED BY SHELL GROWTH

A species is able to grow and reproduce as long as its functional range (biospace) is not exceeded by the ambient environment. Not all parts of the realized biospace promote equal growth or fecundity. Different combinations of niche parameters will be expressed as changed rates of growth, survivorship, or reproductive success. Suboptimal conditions can lead to ecological stress. When broadly defined in this way, ecological stress is probably responsible for many ontogenetic and demographic[1] patterns discussed in this volume.

Although we are addressing ontogenetic growth records and demographic parameters in general terms, we will illustrate these two sources of information in the following paragraphs by drawing examples from the Bivalvia where ontogenetic and demographic shell features are well known.

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[1] Demography, taken literally, means writing about the people (Gr. *dêmos*, the people + to write). The term was originally used to describe statistical studies of human populations; births, deaths, marriages, etc. We use demography in a broader sense; the statistical description of populations of any taxonomic group.

Ontogenetic Growth Records

In the context of this book, we will define ontogenetic growth as the life history of an individual as it is preserved in mineralized, or otherwise refractory, tissues. The ontogenetic history of an organism can be preserved in the shell in several forms. In order for a change in the external environment to be recorded in the molluscan shell, the physiology of the organism must be altered. A metabolic response to an environmental change may, in turn, promote a biochemical response in the mantle and its associated pallial fluid (Chapter 2). Such an external environmental change can then be expressed in the shell. Many physiologic changes are preserved in the shell as growth increments, growth discontinuities, changes in shell allometry, structure and mineralogy. These shell features can be observed on the whole shell or studied from specially prepared shells (See Appendices).

One of the features of the shell most frequently used in the study of ontogenetic growth is internal growth increments and patterns of increments. In molluscs, thin increments, up to tens of microns in thickness, of calcium carbonate-rich growth layers alternate with organic-rich layers. The time span represented by these increments varies between organisms and habitats, but lunar and solar days are commonly recorded in shallow water species. These increments can be seen with a microscope in appropriately prepared cross-sections of the shell (Appendices 1 and 2). No consistent nomenclature exists for the description of these growth features. They have been variously described as internal growth increments, microstructural or microscopic growth increments, or simply as microgrowth increments. The prefix micro is used to distinguish them from macroscopically visible growth "annulations" or bands seen on the external surfaces of many shells.[2]

Microscopic growth increments, observed in thin-sections of shell material, are determined by changes in the ratio of calcium carbonate to organic material. This is seen as a change in optical density of the shell. In acetate peel replicas of sectioned and acid-etched shells, this compositional periodicity results in differential etching of the shell and so the compositional change is observed in the peel as a topographic feature. Boundaries of increments can be gradational or abrupt. In the latter case, they may represent periods of non-decomposition or an erosional unconformity produced through shell dissolution. These growth interruptions are sometimes called breaks, biochecks, or simply checks. They can be periodical, as in the case of shell resorption at each low tide, or aperiodical related to occasional predator attack or disturbance caused by storm turbulence. Physiological changes may also be reflected in the shell as a change in shell microstructure, for example, nacreous, prismatic, or crossed-lamellar structures, and/or a change in shell mineralogy and chemistry (Chapter 2).

In summary, environmental change may be recorded in the skeleton as a change in shell shape and form, microgrowth increments, shell microstructure, mineralogy, or chemistry. A specific environmental change may involve one or several of these variables. At the present time, most shell growth research is attempting to relate observed changes in these shell variables to specific environmental factors.

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[2] Macroscopic growth bands observed on the surfaces of many shells may be a surface expression of closely spaced internal growth increments. Not all species have surface expressions of their internal increments.

Ontogenetic growth studies involve correlating ecological stress factors such as temperature, salinity, dissolved oxygen, food concentration, substratum conditions, and water turbidity with the shell growth record. This may involve experimental manipulation of these variables in the laboratory or consist of correlating seasonally changing field conditions with growth of _in situ_ populations. In some cases, transplantation of individuals from one habitat to another can provide interesting information about site-specific factors on ontogenetic growth.

The ontogenetic approach is not limited to the analysis of internal patterns of growth. One can compare allometric changes in overall external shell dimensions as measured over relatively large intervals of shell growth (usually annual) (Chapter 1). Shell sections representing a complete record of ontogenetic growth are difficult to obtain in three-dimensionally coiled shells (e.g. spired gastropods). With spired shells, ontogenetic information must be obtained from external shell features.

Another ontogenetic approach concerns the earliest growth stages: larval and early juvenile shells. The size, ornamentation, and shape of molluscan protoconchs and prodissoconchs can be used to infer larval developmental types, time of metamorphosis, and dispersal potential (Chapter 4). In some cases, once the larval developmental type has been determined from the features of the top shell, it is possible to make further inferences about adaptive strategies, and hence, the response of an organism to past, present, or future ecological stresses.

Demographic Parameters

Demographic records of environmental change are based on the response of populations to temporal and spatial gradients in environmental quality and ecological stress (Chapter 5). Such changes may be measured as changes in growth rate, recruitment, or survivorship as estimated from size or age-frequency distributions of shell parts.

A one-time collection of a population will reflect the instantaneous age structure of that population. By making several such censes, spaced over at least one year, population recruitment, growth, and mortality can be assessed. Estimates, of these parameters, made from size or age-frequency histograms can be checked by using mark and recapture techniques. Population responses to specific environmental change can be experimentally explored in the field by making reciprocal transplants between habitats. Observed changes in demographic parameters are population measures of relative ecologic stress between habitats.

III. SHELL GROWTH APPLIED TO ECOLOGICAL PROBLEMS

A wide range of ecological problems can presently be approached with shell research. Because research is still at an early stage of development, this range will undoubtedly expand in the future. In the following paragraphs we have outlined applications which we feel can presently be made with current knowledge and techniques. In some of our examples, skeletal research has already proven to be fruitful. In these cases we have identified chapters that explain these applications in greater detail. In other examples, we have had to speculate as to the future potential value of skeletal research because to date, some problem areas remain unexplored.

The response of living organisms to changing environmental conditions is often explored by utilizing census sampling techniques; populations are sampled several times a year to define and follow recruitment patterns and population growth and mortality. Mark and recapture techniques are sometimes also employed to follow ontogenetic growth. These techniques are time-consuming and expensive because sampling must be carried out for at least one year. When completed, the results are applicable to only the year of study. This kind of approach is, of course, the only one available for organisms without skeletal parts. However, skeletonized organisms contain a great deal of ontogenetic and demographic information stored within their exoskeletons. Long-lived species may contain ontogenetic growth records which extend backward in time for several years.

After-the fact Pollution Studies

If a pollution event is sublethal, the effect of the pollutant(s) on ontogenetic growth and reproductive cycles can be deduced from analysis of ontogenetic shell growth records. Demographic analysis may also provide information about subsequent recruitment success and population growth. In the case of sublethal impacts, it is important to choose a species for study whose distribution extends beyond the limits of the polluted area so that ontogenetic and demographic data can be compared between affected and ambient populations.

If the pollution event is lethal to at least some members of a species population, the season of death and age at time of death can be reconstructed for the death assemblage by noting the location of the shell edge relative to the seasonal pattern of internal growth patterns. Survivorship information provided by demographic analysis can identify those year classes that were killed relative to the total age-class structure of the affected population.

For this kind of work, large long-lived species such as *Mercenaria mercenaria* or *Mytilus edulis* are ideal candidates for study as their long life spans allow analysis of skeletal records that encompass pre-disturbance growth conditions as well as post-disturbance recovery.

Identification of Adaptive Strategies

Shell growth parameters can be used by both the neontologist and paleontologist to recognize adaptive types. Opportunistic (pioneering) species have high intrinsic rates of population increase, high rates of ontogenetic growth, and high dispersal capability. Opportunists usually have short life spans and therefore reproduce at an early age. Mortality rates are also high. Equilibrium species have slower rates of population and ontogenetic growth.

Birthrates are commonly balanced by death rates. All of these life history phenomena are capable of being deduced from ontogenetic shell growth, larval top shells of molluscs, and from population shell growth parameters. Shell growth analysis can provide an efficient means of extracting this dynamic information. Once this is done, a sympatric association of species can be ordered into a relative spectrum of opportunism. With such a species ranking, one can make inferences about the role of each species in colonizing new, or newly disturbed, habitats (Chapters 4 and 5).

Fisheries Management

Fisheries management can also benefit from growth studies. Fish scales and otoliths have, for some time, been used to age fish, and this data has proven useful in the management of finfisheries. The application of detailed shell growth analysis to shellfisheries has, as yet, not received the attention it deserves. The shellfisheries biologist is primarily interested in optimizing recruitment and maximizing the yield of soft-tissue biomass. Shell growth can reflect changes in soft-tissue biomass, but only indirectly. During cold months, some molluscs, for instance, experience negative growth of soft tissues, while the shell, although being deposited very slowly, experiences positive growth. In other molluscs, both soft and calcified tissues may experience negative winter growth (e.g. Chapter 2). Poor correlations between changes in shell growth and soft-tissue biomass may also result when gametes are released. Soft-tissue biomass may decrease precipitously during spawning while this reproductive event is recorded in the shell by only a few disturbance lines (Chapter 3). During the period of summer growth, increases in soft-tissue biomass are usually positively correlated with maximum rates of shell deposition.

Shell growth is probably best used in shellfish management to construct ontogenetic and population growth curves. The ontogenetic curve can be used to determine the age at which growth becomes asymptotic to the time (age) axis (Chapter 1). The time or age of maximum yield, in terms of population growth, can also be determined from a demographic analysis of growth. Finally, the age of first reproduction, and the subsequent reproductive history, can often be deduced from spawning lines in the shell (Chapters 2 and 3). By relating these spawning lines to the seasonal clustering of internal growth patterns one can plan the schedule of harvest so that the reproductive potential of the species is not compromised.

IV. PLAN OF THE MANUAL

Chapter 1 is a review of the gross morphology of the bivalve shell, its relationship to soft-part anatomy, and the effect of the environment on macroscopic features of shell growth and allometry. This macroscopic perspective is important for the four chapters that follow.

The molluscan mantle, and the pallial fluid, are responsible for the formation of the shell and its microstructures. Unless the physiological basis of shell deposition and dissolution are well understood, one cannot go very far in interpreting how environmental changes may be recorded in shell growth. Under certain physiologic conditions, part of the interior shell surface may be dissolved. In the process of shell dissolution and subsequent redeposition, primary shell architecture is sometimes reworked into distinctive secondary structures (Chapter 2). These reworked shell layers provide an important datum for reconstructing an organism's physiologic history (Chapters 2 and 3).

Internal ontogenetic growth patterns in marine bivalves have been the focus of considerable research. Detailed descriptions of these patterns, and how they may be used to reconstruct environmental change, as well as the physiology, metabolism and reproductive history of a bivalve, are given in Chapters 2 and 3.

The earliest growth stages of molluscs are often preserved in the umbonal or apical top shell of post-metamorphosed individuals. The size, shape and ornamentation of the top shell can be related to larval developmental type. The larval developmental type, in turn, strongly influences the dispersal potential of a species and allows one to make inferences about a species' adaptive strategy. The ecologic and paleoecologic significance of bivalve and gastropod top shells is discussed in Chapter 4.

Chapter 5 is an introduction to the construction and interpretation of size (age)-frequency distributions and population growth and survivorship curves for both living and fossil molluscs. This chapter shows how comparisons of demographic parameters in space and time can provide useful insights into population responses to environmental change.

CHAPTER 1

SHELL GROWTH AND FORM

by

Raymond Seed

Department of Zoology
University College of North Wales
Wales, U.K.

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CHAPTER 1

I. INTRODUCTION

The Bivalvia constitute the second largest class within the phylum Mollusca. This exclusively aquatic group is exceedingly diverse, and includes species of considerable economic and ecological importance. Bivalves have had a long and supremely successful evolutionary history in which comparatively few lineages have become extinct. Although widely distributed, their apparent preference for shallow water habitats makes them particularly amenable to detailed investigation.

In order to interpret the functional morphology and paleoecology of fossil bivalves, paleontologists depend to a great extent on a thorough knowledge of Recent taxa. Because many fossil bivalves have closely related living representatives, comparisons between Recent and fossil taxa can be made with perhaps a greater degree of confidence for the Bivalvia than is possible for virtually any other group of organisms. By paying particular attention to the ways in which living bivalves respond to environmental change, the paleontologist can draw a considerable amount of valuable information concerning not only the functional nature of fossil taxa but also the environmental conditions of the ancient biospheres in which these taxa evolved. At the same time, however, considerable care must be exercised with such an ecological approach because specific morphological structures may prove to have several distinct functions. This should serve as a caveat to those who may be too willing to generalize about bivalve form and function.

The presence of an accretionary exoskeleton in bivalves in which the total sequence of growth stages throughout ontogeny are recorded, provides an opportunity for analysing the effects of environmental change on shell growth and form throughout ontogeny. In this chapter several aspects of bivalve growth as observed macroscopically (microscopic growth patterns are considered in Chapters 2 and 3) are reviewed and both their ecological and paleoecological implications are briefly considered. Firstly, however, the characteristic features of a generalized bivalve shell will be described and the major evolutionary themes within the class Bivalvia summarized. Ontogenetic and environmentally induced variation in growth rate and body form are considered within the constraints that are imposed by an immutable accretionary skeleton. I use the term immutable only in the sense that the gross morphology cannot be changed once the shell is deposited; the bivalve shell is mutable only at the growing margins. The final section of this chapter is devoted to an analysis of the functional (adaptive) nature of shell morphology in bivalves which differ markedly in their respective modes of life.

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II. GENERAL FEATURES OF THE BIVALVE SHELL

The bivalve shell consists of three distinct parts--two laterally compressed calcareous valves united dorsally by means of an elastic ligament. This comparatively simple construction which grows by the accretion of shell material around the valve margins is, as we shall see later, subject to considerable ontogenetic, as well as phylogenetic, variation. Wainwright (1969) considers that the shape and surface texture of the bivalve shell are advantageous design features in a structure which is subject to continual mechanical stress. However, before reviewing shell growth and form, I shall first of all consider some of the basic terminology used for describing the morphology of bivalve shells.

Figure 1 illustrates the major morphological features and axes of orientation of a generalized bivalve mollusc. The areas of shell immediately surrounding the growth centers or *beaks* of each valve constitute the *umbones* (sing. umbo). These generally raised, somewhat convex regions, often bear traces of the larval shell or prodissoconch (see Chapter 4). They may be curved anteriorly (*prosogyrate*) or posteriorly (*opisthogyrate*) or they may be positioned so as to directly face each other (*orthogyrate*). Where the umbones are widely separated the space between them is termed the *cardinal* area but this may be reduced to an anterior heart-shaped *lunule* and a posterior *escutcheon* in shells with closely opposing umbones. Carter (1967b) discusses the structural and functional significance of these two differentiated regions which are generally set apart from the rest of the shell by a change in surface sculpture.

Dorsally the valves are united by a three-layered elastic *ligament* which consists largely of the horny proteinaceous material conchiolin. The ligament is an integral part of the bivalve shell and is secreted by the underlying mantle tissue in much the same way as the shell valves. It functions like a spring and serves to open the valves when the adductor muscles relax. This it does via the energy stored in it during its elastic deformation whenever the valves are adducted. Where the ligament is external it is generally positioned behind the umbones, but when an extensive cardinal area is present it may extend on both sides of the umbones. Internal ligaments are usually more condensed and often set within shallow pits or *chondrophores* immediately below or to one side of the umbones. Because external ligaments are stretched and internal ligaments compressed during shell closure, the terms *tensilium* and *resilium* are sometimes applied respectively to these two structures. The diversity, functional design, and mechanical efficiency of various types of bivalve ligaments are reviewed by Trueman (1969).

Situated on the inner surface of the dorsal region of the valves immediately beneath the umbones is the *hinge* which functions during the opening and closing of the shell. Along the hinge is a series of *teeth*, the number and arrangement of which are important taxonomic features. Although the two valve surfaces closely interlock at this juncture they are always separated by a neck of tissue, the mantle isthmus, which is continuously enlarging the teeth and deepening the opposing troughs as the shell grows. Hinge teeth ensure that the valves are correctly aligned when the shell closes; they also prevent rotational and shearing movements of one valve over the other. The taxodont condition, found in the Nuculacea and Arcacea is probably the simplest and most primitive type of hinge. Here numerous small, uniform, straight or chevron-shaped teeth occur over the entire length of the hinge. The more common and more highly developed heterodont hinge consists of distinctly differentiated cardinal and lateral teeth which diverge from a point immediately below the umbones. The taxodont and heterodont conditions, along with various other types of bivalve dentition are detailed by Cox (1969). In some taxa, hinge teeth may be reduced or even absent.

Muscle scars present on the inside of the shell can sometimes provide valuable information concerning the structure of soft parts and the life habits of bivalves. Furthermore, as many of these scars are frequently well preserved in fossil material they provide a potentially important paleoecological tool. Extending around the inside of the valves near the shell margin is the pallial line representing the point of attachment of the shell-secreting mantle lobes. In taxa with posterior siphons, the pallial line may be indented forming a pallial sinus into which the siphons can be withdrawn by means of the siphonal retractor muscles (enlarged pallial muscles). The size of this sinus broadly reflects the strength and extrusibility of the siphons and the degree to which they are fused together, rather than their overall length (Kauffman 1969). Valuable inferences about modes of feeding and burrowing depths can be made from the nature of the pallial sinus. The largest and perhaps most important muscle scars on the inner shell surface are those produced by the adductor muscles because the spatial orientation of many other features of the bivalve body can be related directly to these reference points. As the adductors are responsible for valve closure their action directly opposes that of the elastic ligament. Each muscle consists of two functionally dissimilar fibers and the precise extent of these "quick" and "catch" components can occasionally be identified by careful inspection of the scar. Owen (1958) and Yonge (1953) suggest that the adductor muscles probably originated through cross connections of pallial muscles at the ends of the mantle embayments in the ancestral bivalve. Typically there are two adductor muscles present, one anterior and one posterior. This constitutes the dimyarian condition. These muscles may be similar in size (isomyarian) or the anterior muscle may show varying degrees of reduction (anisomyarian or heteromyarian). Alternatively there may be only a single posterior adductor muscle present (monomyarian). Although the latter may be more or less centrally positioned, careful inspection shows that it is always set slightly posterior to the midline. Various other muscle scars such as those associated with the foot or byssal complex, and the small cruciform muscle characteristic of the Tellinacea, may also be identified by careful inspection of the shell, and these too furnish further valuable information concerning taxonomy and life habits. The arrangement and functional significance of many of these shell-attached muscles are described in some detail by Cox (1969) and Kauffman (1969).

Any study of comparative morphology requres a terminology related to growth axes. However, because bivalves lack a distinct head, confusion can easily arise over what constitutes the anterior-posterior axis of the body. For descriptive purposes it is convenient to consider the hinge to be dorsal in position and to orientate anterior and posterior regions with respect to the hinge axis (i.e. the axis along which the valves open and close). Previous workers have also defined the anterior-posterior axis by reference to lines drawn through the lower margins of the adductor muscles or through the mouth and anus. The former method is of little value in the case of monomyarian taxa while the latter clearly has limited potential for fossil material (though it is worth noting that the anus almost invariably opens over the posterior adductor muscle). Even the hinge axis may not always be easily determined, especially in bivalves with condensed ligaments and Cox (1969) proposes that measurements of length and height (Fig. 1) should simply reflect the maximum shell dimensions between the anterior and posterior and the dorsal and ventral margins of the shell irrespective of the exact direction of measurement. Shell width is the maximum distance between the two valves measured normal to the plane of articulation (see commissure definition below). For sectioning purposes (see Appendix 1) an additional growth axis can be recognized. This is the "axis of maximum shell growth" and represents the maximum dimension between the umbo and the growing edge of the shell. Figure 1D shows this growth axis for two dissimilar bivalves.

Where one valve is a virtual mirror image of the other, the shell is described as equivalve; inequivalve when the valves are dissimilar. When regions of the shell anterior and posterior to the umbones are of approximately equal size the shell is equilateral; inequilateral when these regions differ appreciably. Externally the bivalve shell can vary extensively with regard to color and the degree of ornamentation. The line of junction between the two valves, but excluding the region of the ligament, is the commissure. Localized openings which remain between the valve margins when the adductor muscles are fully contracted are termed gapes and these too can have considerable interpretive value. While the shells of most bivalves consist of two valves, various accessory plates or calcareous pallets may also be developed amongst those taxa which bore into rock or timber.

III. ORIGIN AND EVOLUTION OF BIVALVES

Although bivalves are known to extend at least as far back as the Ordovician (e.g. Morris 1967; Pojeta et al. 1972; Stanley 1977) their precise origins are far from clear as they were already quite distinctive by the time they first appeared in the fossil record. A considerable and significant chapter in the evolution of bivalves thus appears to have occurred prior to shell calcification and their early ancestry must therefore remain rather speculative. Morton and Yonge (1964) consider that the forerunners of bivalves probably had single, uncalcified limpet-like shells which were attached to the visceral mass by a series of muscles running down to the foot. Originally several pairs of these muscles may have been present, as indeed they appear to be in Babinka, an Ordovician bivalve (McAlester 1965; Stasek 1972). However, these shell muscles have gradually become restricted to two pairs of pedal muscles in Recent taxa (four pairs in the more primitive Nuculacea). The development of the typical laterally compressed bivalve form led to the appearance of anterior and posterior embayments in the shell across which the characteristic adductor muscles developed by local fusions of the pallial muscles. The enclosure of the body between two compressed valves secreted by the underlying mantle folds led to the reduction of the head and its associated radula complex while sense organs became arranged around the mantle periphery where they could best sample the water currents entering the mantle cavity. Carter and Aller (1975) suggest that the immediate precursors of the bivalves may have been shell-less spiculose molluscs while Runnegar and Pojeta (1974) propose a monoplacophoran ancestry.

We can only speculate as to the probable life style of these early bivalves. It is widely believed (e.g. Pojeta 1971; Yonge 1953a) that their early evolution occurred in littoral or shallow sublittoral deposits through which they moved by means of their muscular hydraulic foot. These early bivalves probably fed on organic deposits using extensions of their oral palps in much the same way as present day protobranchs. In support of this infaunal origin is the observation that most modern taxa, irrespective of their life styles as adults, do possess features during their early ontogency which would ideally suit them for a burrowing existence. Moreover, the earliest known bivalve Fordilla troyensis is thought to have been a prosogyrate burrower (Pojeta et al. 1973). Tevesz and McCall (1976) however, believe that the earliest bivalves may in fact have been epifaunal suspension feeders rather than burrowers (see also Valentine and Gertman 1972). Tevesz and McCall (1976) suggest that bivalves arose at small body size (Ca. 1 mm) when those features generally considered to be adaptations for burrowing can also be used for crawling over the surface of the substratum. This is particularly well illustrated among the tiny erycinaceans and the pediveliger stages of bivalves such as Mytilus. The development of the bivalve shell, which is also found in many small primitive crustaceans, probably afforded substantial protection from meiofaunal predators, better control of the internal environment, and more efficient circulation of water currents through the mantle cavity. Apart from those theories outlined above, a multiple origin ancestry has also been proposed to explain the early evolution of bivalves (e.g. McAlester 1966; Vokes 1967).

Present day bivalves fall into three groups. The primitive deposit-feeding protobranchs (e.g. Nucula, Yoldia), which probably represent a continuation of the ancestral stock, and the carnivorous septibranchs (e.g. Cuspidaria, Poromya) which are specialized for life in deeper nutrient-poor waters, are small groups compared with the more diverse lamellibranchs. By utilizing highly developed gills (ctenidia) for both respiration and feeding the diverse and exceedingly successful lamellibranchs have freed themselves from the constraints of deposit feeding (although some taxa have in fact reverted to this life style) and have undergone considerable adaptive radiation in numerous aquatic habitats. The dependence of bivalves on gills and pelagic development, however, has effectively prevented them from becoming established in terrestrial habitats.

Two major evolutionary events have largely been responsible for the successful radiation of bivalves--the neotenous retention of the post-larval byssus complex and the development of siphons accompanied by varying degrees of mantle fusion. The byssus gland (a modified pedal mucous gland) originated as a post-larval organ used for temporary attachment during metamorphosis (Yonge 1962). Once metamorphosis has been completed, the byssus gland is frequently lost, but its retention into the adult stages in many bivalves (by neoteny) was instrumental in the colonization of epifaunal habitats and permitted many diverse taxa to become independent of soft sediments. The colonization of hard surfaces using a system of proteinaceous byssal threads for attachment has had a profound influence on bivalve shell morphology. It has resulted in considerable shell asymmetry and the gradual reduction (*anisomyarian*) and eventual loss (*monomyarian*) of the anterior adductor muscle. Byssal attachment, which evolved polyphyletically in many different groups (e.g. Mytilacea, Arcacea, Anomiacea, Pteriacea), led, in turn, to the appearance of cemented taxa like oysters (Ostreacea) and perhaps most surprisingly, to free swimming groups like many of the scallops and file shells (Pectinacea), many of which have secondarily reverted to a more symmetrical shell form. Boring into the substratum confers considerable protection from water movement and predation and is known to have evolved by two independent routes, one of which was byssal attachment. Some byssate taxa, such as the fan shells (e.g. *Pinna*), have re-invaded sediments after having evolved many of the shell characteristics more typically associated with life on hard substrata (Yonge 1953b). Reversion to an infaunal way of life has probably occurred many times during bivalve evolution and this too may have been via neoteny as the post-larval stages of byssate taxa still retain an active burrowing foot. Considerable evolutionary potential is thus stored in bivalve larvae (Stanley 1972; 1977).

By contrast with byssally attached forms, bivalves inhabiting soft sediments are much more conservative in their shell shape. Nevertheless, considerable radiation in life habits has occurred, principally through the development of siphons and varying degrees of mantle fusion. Infaunal taxa are especially successful and account for well over three quarters of all living bivalves (Table 1). Apart from the very specialized and rather aberrent Lucinacea (see Allen 1958; Kauffman 1969), deeply burrowing infaunal suspension-feeding bivalves were virtually unknown in the Paleozoic, and fossils from these strata rarely have a pallial sinus (Stanley 1968). The development of siphons (Yonge 1948; 1957) opened up many new habitats by permitting infaunal bivalves to penetrate much deeper into the sediment. Life deep in the substratum led to improved physical stability, reduced the risk of disinterment, and provided considerable protection from predators. An important comparison of infaunal and epifaunal environments is given by Levinton (1972). Siphon formation also provided for a much more orderly flow of water through the mantle cavity and when accompanied by mantle fusion resulted in a more effective hydraulic system both for burrowing and siphon extension. The vast majority of suspension-feeding bivalves draw water (and food) into the mantle cavity through a posterior inhalent siphon (anterior in the Erycinacea). They may live near the surface and possess short siphons (e.g. Carditacea, Veneracea) or they may be deep burrowing forms with either massive fused siphons (e.g. Myacea, Mactracea) or elongate shells (e.g. Solenacea). They can be sedentary or they can be active burrowers. Each life style imposes its own suite of morphological features on the bivalve shell. The siphonate tellinaceans have reverted to the ancestral condition of surface deposit feeding and acquire their food either from the surface or from within the sediment itself. Unlike the more primitive protobranchs, however, food is here collected by means of extremely long, mobile inhalent siphons which sweep the sediment like miniature vacuum cleaners. These active deposit feeding siphonates are exceedingly successful especially in rich organic muds to which they are adapted. Just as byssal attachment provided a route for the evolution of the boring habit, so too did certain adaptations for deep infaunal burrowing because many of the features which evolved for deep burrowing are also equally adaptable to a life spent boring into hard substrata.

For many millions of years after their first appearance bivalves remained at a relatively low level of species richness (Stanley 1975a; 1977). Their rapid expansion during the Ordovician thus appears to have been marked by the neotenous retention of the versatile byssus complex. Epibyssal attachment opened up the route for numerous diverse life styles including free swimming. Tevesz and McCall (1976), suggest that this Ordovician expansion followed the adoption of an infaunal habit by small primitively epifaunal bivalves. Moreover, apart from resulting in rapid taxonomic diversification, the invasion of this new adaptive zone could also explain the substantial increase in body size which is known to have accompanied this expansion. Recolonization of hard substrata by byssally attached fauna may thus have occurred later in the Ordovician at larger body size. Thayer (1979) considers that the diversification of immobile taxa living on hard surfaces, and mobile taxa on soft substrata, is possibly attributable to the increased amount of bioturbation brought about by the increase in the abundance and diversity of mobile deposit-feeding taxa during the Paleozoic. Perhaps one of the most striking features concerning the evolution of such a diverse group as the bivalves has been the repeated appearance of a comparatively restricted number of very successful shell morphologies. The fact that many primitive taxa have persisted while many modern taxa have reverted to more primitive life styles has led Stanley (1973; 1977) to conclude that competition, unlike predation, has been a comparatively weak selective force in bivalve evolution.

IV. SHELL GROWTH

Although the principal objective of this chapter is to examine the relationships between shell morphology and environmental change, I shall set the study of shell shape within the broader context of overall shell growth. This is considered appropriate as the shape of any bivalve shell depends ultimately upon growth processes. Furthermore, growth and size have, in themselves, several important ecological and evolutionary implications.

Growth has been extensively studied in bivalved molluscs not only because of the commercial importance of groups such as oysters, clams and mussels but also because their growth history can often be observed on the external surface of the valves in the form of disturbance rings. This latter feature, in particular, makes bivalves especially suitable for growth studies. Two principal methods have previously been used to represent bivalve growth: (i) the size of the whole organism can be related to age, (ii) the growth of one shell parameter can be related either to that of another parameter or to the whole body. These methods will each be examined in turn:

Absolute Growth

By taking successive measurements of animals of known age it is possible to construct a growth curve. The cumulative increase in body size with respect to time which is represented by such a curve is termed absolute growth. The percentage increase per unit of time provides a measure of relative growth. While the growth of living organisms is most appropriately measured in terms of increase in biomass or volume, the shell is such a prominent feature of the bivalve mollusc that growth is more frequently expressed as increase in shell length. This is also convenient for the paleoecologist as it allows direct comparisons to be made between living and fossil taxa. In comparative investigations, however, caution should be exercised in using single linear parameters to measure growth rates. For example, although two individuals may be increasing in their total biomass at an approximately equal rate, their growth in terms of other parameters such as length, height or width may vary quite considerably according to age and/or environmental conditions. Furthermore, there is also the additional problem that, during winter, soft tissues may experience negative growth while shell continues to be deposited.

Several methods are available for assessing growth rates in bivalves. These include the use of modal size-frequency distributions, the use of annual disturbance lines where these are present on the shell, and the measurement of marked or segregated individuals. Other methods including X-ray techniques (particularly useful for boring species) and rates of incorporation of radioactive isotopes or fluorescent dyes into the shell, are discussed by Wilbur and Owen (1964). Several of these techniques have been used to study growth in the mussel Mytilus edulis but Seed (1976) concludes that probably the most reliable estimates of growth have been those obtained using a combination of methods. Recent analyses of internal shell growth increments in bivalves (Chapters 2 and 3) appear to offer considerable potential for high resolution growth studies in both Recent and fossil taxa (e.g. Clark 1974; Lutz 1976; Pannella and McClintock 1968). Microgrowth patterns within the shell record a variety of environmental changes and therefore have many ecological and paleoecological applications.

A habitat, by virtue of its resource-limiting environmental conditions, imposes a maximum size beyond which further growth can proceed only very slowly, if at all. For example, when mussels which have more or less attained the maximum size imposed by a particular environmental regime are transplanted to more favorable conditions they respond by a further period of enhanced growth (Seed 1968) until the assymptote characteristic of the new environmental regime is approached. The maximum attainable size ($L\infty$) under any set of environmental conditions can be approximated by means of the Ford-Walford plot (Beverton and Holt 1957; Hancock 1965). This parameter is basic to many growth equations, one of which, the von Bertalanffy, has been widely used for various bivalve taxa. Here:

$$Lt = L\infty \ [1-e^{-kt}]$$

where t = time, $L\infty$ = maximum size and k is a growth constant. Equations of this type, however, are based on determinate[1] growth, while growth in many bivalves may not, in fact, be determinate at least over their realized life span and may not, therefore, cease at any particular fixed adult size. Despite criticisms (e.g. Knight 1968), curve fitting by means of growth equations is perfectly acceptable, providing (a) that data are relatively complete, i.e. there is at least some evidence for assymptotic growth, and (b) that it is appreciated that some uncertainty is always associated with such estimates. Table 2 compares the values of $L\infty$ and k among various populations of Mytilus edulis and illustrates low rates of growth associated with overcrowding, the low growth rates in Greenland compared with other North Atlantic locations, and the relatively large sizes attained by Arctic mussels.

One of the most striking features of bivalve growth is the degree to which it varies with respect to age and environmental conditions (Fig. 2). While patterns vary from species to species, bivalve growth curves are characteristically sigmoidal in shape, the initial exponential phase of growth being followed by a gradual decline as the animal ages. This decline in growth occurs to such an extent that in very old individuals growth may virtually cease. Senility, however, is not necessarily the primary cause of reduced growth because transplantation of old slow-growing animals to more favorable habitats generally results in renewed growth. Numerous environmental factors, e.g. food supply, temperature, substratum, salinity, light, depth, turbidity, population density (crowding) and exposure to high energy environments are known to influence growth rate in bivalves. The effects of these and other factors are discussed by Hallam (1965), Rhoads and Pannella (1970), Seed (1976), and Wilbur and Owen (1964). However, it is frequently difficult to isolate the important causal factors, especially as all variables are not independent of each other. Even individuals of similar size and/or age grown under apparently identical conditions can vary considerably in their growth rates and there now seems to be some evidence to indicate that growth (and indeed survival, Newkirk et al. 1977) is at least partly determined by genotype (Singh and Zouros 1978; see also Murdock et al. 1975). Hallam (1965) considers that an examination of those factors causing stunting could be a potentially important interpretive technique, assuming that juveniles and stunted adults could be distinguished, by providing important data regarding paleoenvironmental conditions and the physical tolerances of many taxa. This is perhaps an overly optimistic view, especially for bivalves whose growth rates may vary within extremely broad limits even on a comparatively localized scale. Quite apart from the formidable task of disentangling all potentially important variables, the question of adaptation would also need to be considered. Some species, for example, appear to thrive in comparatively anaerobic sediments or in waters of exceedingly low salinity, i.e. in environments that are generally considered to be unsuitable for bivalves. Furthermore, body size is subject to natural selection and is known to change over evolutionary time (e.g. Bonner 1968; Hallam 1960).

Growth rate in several molluscs is known to vary with latitude (Newell

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[1] Determinate growth indicates that some maximum attainable size exists for any given population. Species exhibiting indeterminate growth, by contrast, continue to grow throughout their entire life span.

1964). Whilst populations from higher latitudes exhibit slower growth rates due to lower temperatures, longevity and ultimate size in these populations are frequently greater than in those from lower latitudes. Hallam (1967) suggests that, where such data could be supplemented by growth ring analyses, the prospects of establishing paleotemperature gradients may be quite promising especially if fossil material were available from comparable horizons over a relatively large geographical area. Lutz and Jablonski (1978, see also Chapter 4) also suggest that the size of veliger larvae at settlement is controlled by gradients in latitudinal temperature. Hence, the size of larval (or early juvenile) shells might also provide evidence for reconstructing paleotemperature gradients. However, considerable differences in size and age may occur even among bivalve populations inhabiting the same general geographical locality. For example, high shore mussels on many exposed rocky coasts occupy a spatial refuge in which they are virtually free from predation (Paine 1974; Seed 1969, 1976). While very slow-growing, these high shore populations frequently include many old, yet comparatively large, individuals when compared with faster growing but more heavily predated populations in the low shore. Moreover, Gilbert (1973) has shown that at higher latitudes longevity increases, whereas growth _and_ maximum size decrease in _Macoma balthica_.

Body size has a number of important ecological and evolutionary implications. Fitness in any individual within a population can broadly be measured in terms of the extent to which it proves superior in propagating its genotype. Those individuals which propagate more of their genotypes by producing most offspring will have a proportionately greater influence on the course of evolutionary change. In most bivalves fecundity is proportional to body size and gamete production in any one year which reduces the capacity for growth has therefore to be weighed against increase in body size and the expectation of a higher fecundity during the following year. Because the amount of energy available to any population is generally limited, there sometimes exists a trade-off between reproductive effort and continued growth. Seed and Brown (1978) have recently shown that the different growth strategies adopted by subtidal _Modiolus modiolus_ and intertidal _Cerastoderma edule_ appear to operate in order to maximize reproductive efficiency within different frameworks of heavy mortality. We have already noted how the high shore can constitute a refuge from predation for certain intertidal species such as mussels. Some bivalves e.g. _Modiolus modiolus_ (Seed and Brown 1978) and _Mytilus californianus_ (Paine 1976) also appear to be able to escape predation by growing rapidly to a size where they are too large to be eaten by any of their major predators. These large individuals then make a reproductive contribution disproportionately greater than their numerical abundance would suggest. They may also influence species richness and community stability by diversifying the spatial structure of the environment through the addition of a vertical component that might not otherwise be present (Paine 1976). Selection would therefore be expected to favor early rapid growth and delayed reproduction in those species which can escape predation by virtue of large size. Growth rate can also influence the outcome of competition between closely related species. Harger (1972) demonstrated that _Mytilus californianus_ can virtually eliminate its major competitor _M. edulis_ from the outer waveswept shores of the Pacific northwest coast of America by virtue of its mechanically stronger and faster growing shell.

An area of particular paleoecological interest is the analysis of size-frequency distributions of living and fossil bivalve assemblages (e.g. Craig 1967; Craig and Hallam 1964; Craig and Oertel 1966; Hallam 1967, 1972; Johnson 1965; Seed and Brown 1975). This field of research is discussed in detail in Chapter 5 and it merely remains to be noted at this point that size-frequency distributions require an adequate understanding of the interactions between the processes of growth, recruitment, and mortality before they can be properly evaluated.

Allometric Growth

Although it is important in any ecological study to establish the rate at which growth proceeds under different environmental conditions, it is clearly evident that body shape does not always change uniformly with an absolute increase in size of the whole animal. Changes in the relative proportions of the bivalve shell with increasing body size are the result of differential growth vectors operating at different points around the mantle edge. The study of the different rates of growth between two parts of the body or between one part and the whole organism is termed allometry. The concept of allometry was first proposed by Huxley and Tessier (1936) and its contributions to developmental and evolutionary biology are critically reviewed by Gould (1966). One of the most significant effects of growth follows from the simple geometrical principle that while the area of a body increases as the square of its linear dimensions, volume increases as its cube. Thus if geometrical similarity is maintained throughout growth, the area to volume ratio will progressively decline. However, because most exchanges between the external environment and the organism occur across body surfaces, relatively constant area to volume ratios are an adaptive necessity and these can only be maintained by changes in shape. Form is thus inextricably related to body size.

The relationship between any two parts of the body can be expressed by the power function:

$$y = Ax^b$$

where y is a measure of one part and x that of another part or the whole body. A and b are constants. The exponent b in this equation is the growth coefficient and represents the relative growth rate of the two size variables under consideration. The constant A is calculated as the value of y when x is unity. This is the allometric equation which, in view of its simplicity and the relative ease with which it can be interpreted, has found wide applicability amongst biologists. Although more sophisticated functions (e.g. polynomials) can be used to describe growth data, Gould (1966) questions whether such techniques add substantially to our understanding of biological processes. Rewritten in logarithmic form the allometric equation becomes:

$$\log y = \log A + b \log x$$

such that if y and x are allometrically related they plot rectilinearly on logarithmic coordinates. The slope and intercept of such logarithmically transformed data are given by the constants b and A, respectively. When the two variables being considered have the same units of measurement, a value of unity for the exponent b is said to describe an isometric relationship in which the relative growth of the two variables is identical, thereby maintaining geometrical similarity with increasing size. Values of b greater than unity indicate that y is increasing relatively faster than x (positive allometry) while values of b less than unity indicate the reverse (negative allometry). If the dimensions of x and y differ then different criteria for isometry and allometry will apply, e.g. where y is a weight or volume (L^3) and x is a length (L) then b = 3 corresponds to isometry. Growth coefficients for several combinations of size parameters for three species of bivalves are shown in Table 3. The relative constancy of the allometric exponent over a wide size range indicates that while the two variables may themselves have different rates of increase, the ratio between these rates remains relatively constant.

The use of bivariate data in allometric studies is perhaps open to the criticism that only two variables are compared at any given time and, as well as changing their proportions, animals also change their shape. Accepting that such data alone do not satisfactorily describe changes in body form, they do, nonetheless, enable simple and useful comparisons to be made of the variability in shell proportions among different bivalve populations and thereby provide valuable insight into the relationships between shell shape and environmental change in space or time. However, before any environmental control over shell shape can be demonstrated unequivocally it is clearly necessary to establish how much variation is due simply to changes in body size, i.e. the extent to which shape varies during ontogeny.

Although shell growth in certain bivalves such as Glycymeris is virtually isometric (Thomas 1976) most taxa exhibit some ontogenetic changes in shape. Marked alterations in the pattern of growth, as witnessed by relatively abrupt changes in the ratios of various shell dimensions (e.g. Johannessen 1973; Ohba 1959), may indicate that major changes in life habits have occurred during ontogeny. Usually, however, these ratios can be adequately described by a single allometric relation (e.g. Mason 1957; Nayar 1955). Gradual allometric changes with increasing body size are more generally associated with maintaining physiologically favorable surface area to volume ratios rather than with changing environmental conditions. Figure 3A compares the growth of various shell parameters relative to length in the mussel Mytilus edulis and shows that, while in this particular population a more or less linear relationship exists between length and width, the rate of increase in shell height declines slightly in the larger size categories. Weight and volume, on the other hand, are related in typical exponential fashion. When these growth data are plotted on logarithmic axes (Fig. 3B), values for the constants A (intercept) and b (slope) in the allometric equation can be obtained. Apart from volume (b = 3), the values of b in these regressions depart significantly from isometry. Width and shell weight exhibit positive allometry, while height is negatively allometric with respect to shell length. Differential growth between these various shell parameters in Mytilus is thus reflected in a gradual change in shell shape, older (= larger) mussels having relatively heavier, more elongate shells in which width can frequently exceed shell height (Fig. 4). Pohlo (1964) has shown that the ontogenetic changes in Tressus nultalli can be related to differences in life style between the actively burrowing juveniles and the more sedentary adults which live a more protected life deeper in the sediment. Positive allometric growth of the posterior region of the shell is here associated with the increase in space required for the enlarged siphons. Similar environmentally induced ontogenetic shape changes have also been recorded by Kristensen (1957) for Cardium (= Cerastoderma), Johannessen (1973) for Venerupis, and Stanley (1970) for Mercenaria. Brown et al. (1976) recently demonstrated that the species specific changes in shape which occurred in Modiolus modiolus, Cerastoderma (= Cardium) edule and Mytilus edulis appeared to have adaptive significance. Much greater emphasis was placed on shell growth than on tissue growth in the intertidal species (Mytilus and Cerastoderma) than in the subtidal population of Modiolus. Differences in the allometry of the linear dimensions, on the other hand, could largely be explained in terms of the relative degree of crowding experienced by these three bivalves. Because growth rate in bivalves is known to vary widely from one habitat to another, it should be remembered that individuals of similar size need not be of similar age. The differences in shell weight of mussels of similar length from different tidal levels (e.g. Baird and Drinnan 1956; Seed 1973) can largely be explained in terms of such age differences, the older, slower-growing individuals from high shore populations having comparatively heavier shells than their younger but faster-growing conspecifics lower in the intertidal region.

We have already seen that when weight and length are being compared, $b = 3$ corresponds to isometry. Some bivalves, however, show a progressive increase in their relative bulk density. Enhancing physical stability by increasing bulk density can be advantageous to those species which freely recline on the sediment surface or to shallow burrowers which are subject to frequent wash-out by currents. Increase in shell thickness or strength can also be an effective antipredator device. Heavier shells, on the other hand, can be detrimental to species living on very soft sediments into which they would readily sink and the growth exponent (b) for two mud dwelling bivalves, Mulinia (2.75 ± 0.82) and Nucula (2.57 ± 0.52) is therefore significantly less than 3 (Thayer 1975). Bulk density in these bivalves thus decreases throughout ontogeny. In the wood-boring bivalve Teredo, where the shell merely serves as a cutting tool, the growth exponent ($b = 1.37$) is reduced even further (Isham et al. 1951).

There is an extensive literature concerning the potential influence of environmental change on shell proportions in bivalves. Crowding is known to affect shape in Mytilus edulis diegensis (Coe 1946); Mytilus edulis (Seed 1968, 1978); Pinctada martensii (Tanita and Kikuchi 1957); Venerupis semidecussata (Ohba 1956), and Donax striatus (Wade 1967). Crowding also appears to be the principal cause of the morphological differences that exist between populations of Modiolus demissus which share a comon gene pool (Lent 1967). Mussels from similar but widely separated populations (relatively crowded salt marsh muds), on the other hand, were found to be remarkably alike in their shell proportions. The nature of the substratum is reported to have a marked effect on shape in Venerupis pullastra (Quayle 1952), Mya arenaria (Swan 1952), Crassostrea virginica (Gunter 1938; Orton 1936), Cardium edule (Purchon 1939) and Penitella penita (Evans 1968). Wave impact, trophic conditions, and water depth are also thought to influence bivalve shell shape (e.g. Clark 1976; Eager 1978; Fox and Coe 1943; Orton 1928). Nicol (1967) found that bivalves living below 5°C tended to be rather small with thin chalky skeletons and subdued ornamentation. Fossil assemblages with similar shell characteristics might possibly be interpreted therefore as cold water assemblages. Holme (1961a) showed that in Venerupis rhomboides a linear relationship existed between height to length (H/L) ratios and water depth (possibly caused by hydrostatic pressure) when these were plotted on a logarithmic scale (Fig. 5). By means of this correlation, relatively accurate estimates of water depth could be made solely from a knowledge of shell proportions. Data such as these could clearly provide valuable information concerning the extent of shell transportation along the sea bed and the physical conditions of the original habitats of specimens from both beach and sub-Recent shell deposits. Eisma (1965) found a similar strong correlation between salinity and the number of radial ribs in Cardium edule. However, correlations between shell morphology and environmental paramenters without any knowledge of their functional relationship has the obvious weakness that such correlations, however strong, may not be causal. Morphological features may be correlated with some factor other than the one chosen for correlation and where this other factor does not correlate highly with the chosen parameter then the morphological correlation breaks down and interpretation based upon morphology will be incorrect (Valentine 1973). This is especially true for factors such as depth or latitude which are not in themselves physiological factors.

Considerable evidence is thus available to suggest that environmental change can have profound effects on the shell proportions of a number of bivalve molluscs. That such effects are indeed essentially phenotypic can be demonstrated experimentally by transplanting animals from one habitat to another and recording the resulting changes in shell form (e.g. Clark 1976; Eager 1978; Evans 1968; Rhoads and Pannella 1970; Seed 1968). Figure 6 illustrates the changes which occur in shell proportions and rate of growth when two exposed shore mussel populations are transplanted to less crowded experimental cages at low tidal levels in a sheltered estuary. In a series of experiments using oysters, however, Hasuo (1958) concluded that ecological factors alone may not always explain the observed differences in shell shape. Ontogenetic and phenotypic variation in shell morphology has obvious implications in taxonomic studies. Mistaken identification can easily arise from the assumption that shape is independent of body size. New shapes may simply result from the continuation of allometric trends to larger size, and differences in magnitude may be the only characters separating two otherwise identical forms (Gould 1966). Fossil species, by nature, are morphological taxa and because the assessment of morphological characters is somewhat arbitrarily determined, Wright (1972) suggests that paleontologists are occasionally guilty of overemphasizing morphological trivia. Characters commonly regarded as important taxonomically may eventually prove to be phenotypic. Only after the relationship between water depth and shell shape had been established (Holme 1961a) was it fully appreciated that Venerupis rhomboides is a single, but highly variable, polymorphic species. Mytilus is another extremely plastic species in which shell shape varies both with age and environmental conditions. Such variability renders gross shell morphology a doubtful taxonomic character in this particular taxon (Seed 1968, 1978). Phenotypic variation is probably far more widespread than is generally believed, especially among those species inhabiting less predictable habitats, such as the intertidal and shallow subtidal. In such species the maintenance of wide variation may actually constitute a "functional insurance" for survival in a constantly changing environment (Eager 1978).

V. SHELL SHAPE AND BODY FORM

Most allometric studies of bivalve shell shape have used bivariate data in which only two parameters (such as length, height, or width) are considered at any one time. Although useful for describing the changes in body proportions that occur either during ontogeny, or as a result of environmental change, such an approach does not permit an adequate analysis of total body form. Our present understanding of shell geometry in bivalves is largely attributable to the work of Carter (1967a), Huxley (1932), Owen (1953a,b), Raup (1966), Stask (1963a,b), and Thompson (1942).

In view of its accretionary mode of growth (i.e. by marginal increments), the bivalve shell has generally been considered in terms of a logarithmic spiral, the shape and growth of which has been analyzed in several distinct ways. One of the fundamental properties of logarithmic spiral growth (Fig. 7) is that it permits increase in size to occur without requiring any corresponding change in shape, a feature which, although approached by most bivalves once beyond their immediate post-larval stages, is rarely ever completely realized: most bivalves exhibit at least some degree of ontogenetic change during their shell growth.

Owen (1953b) considers that the direction of growth at any given point along the growing mantle edge can be resolved into radial and transverse components. The radial growth component, represented by lines radiating from the umbones, acts in the plane of the generating curve (represented by the mantle-shell margin), while the transverse component acts at right angles to this curve (Fig. 8). The ratios between these two components defines the spiral angle and thus the degree of concavity of the shell valves. Compare for example, the exceedingly flat shell of tellins with the more obese shells found amongst cockles. The interaction of radial and transverse components is well illustrated in *Glycymeris* where a section passing through the umbones and the middle of the ventral shell margin describes a planospiral about the umbones and in the plane perpendicular to the generating curve. Where the radial and transverse components remain relatively constant, the resulting shell takes on the form of a logarithmic or equiangular spiral (see Thompson 1942), in which growth proceeds without any concomitant change in shell shape. Flat shells, such as the upper valve of the scallop *Pecten maximus*, are generated when only the radial growth component is present.

The shape of the generating curve, which depends largely on the magnitude of the radial growth component around the shell margin, need not be symmetrical as it is *Glycymeris* (Fig. 9a). Different functions associated with the anterior and posterior regions of the shell generally result in varying degrees of asymmetry about the anterior-posterior axis. In bivalves such as *Tivela*, marginal increments may be equally large in both anterior and posterior regions, thus producing a more or less elliptical shaped shell, but in most taxa these increments are greatest posteriorly. Such asymmetrical growth patterns are especially pronounced in the elongate shells of the razor clams, e.g. *Ensis* (Fig. 9c).

In addition to the radial and transverse growth components many bivalves also have a third component which acts tangentially to, but in the same plane as, the generating curve. The effect of this tangential component is to produce a turbinate or twisted spiral, the growth of which is the result of two differential growth ratios, one acting perpendicular to the generating curve, the other (the lateral ratio) acting within the plane of the generating curve (Huxley 1932; Owen 1953). This is best illustrated in shells with radial ornamentation because the ribs are displaced in the direction in which the tangential component acts. Thus, whereas the effects of interaction between radial and transverse components is to produce a planospiral about the umbones in a plane perpendicular to the generating curve, interaction between radial and tangential components produces a similar spiral but within the plane of the generating curve. The form of the bivalve shell results from the interplay of these two systems of spirals (Owen 1953b). In shells with a high spiral angle and no tangential component there is a tendency for the opposing umbones, e.g. in cockles, to grind into one another when the shells are open. Where the tangential component is large, the umbones become displaced either anteriorly (e.g. *Glossus*, *Arctica*) or more occasionally posteriorly (e.g. *Nucula*). Such spiral twisting may sometimes actually cause the ligament to split (Owen 1953a). Raup (1966) and Stasek (1963) examine some of the ways in which the problems caused by juxtaposition of the umbones can be circumvented.

For comparing shell form in different bivalves, extensive use has been made of the demarcation line (= normal axis) which starts at the umbo and passes through the region of maximum inflation of each valve (i.e. where the transverse to radial component is greatest). This line effectively divides the mantle-shell into anterior and posterior territories (Figs. 8,9). Where growth is not influenced by a tangential component, this line has the form of a planospiral, but when a tangential component is present, it becomes a turbinate spiral. The bivalve shell can thus be fully described by reference to the spiral angle of the normal axis, the form of the normal axis (i.e. whether a planospiral or turbinate spiral) and the outline of the generating curve. The demarcation line has been used extensively by Yonge (1953a, 1955) and Owen (1953b, 1958, 1959) for comparing shell form as well as the interrelationship between the mantle-shell and the visceral mass.

While considerable importance has thus been attached to the demarcation line in describing bivalve growth and form, Lison (1949) puts greater emphasis on the directive spiral. This can be seen to greatest effect by reference to ribbed shells like *Pecten* where only one rib follows a completely straight course (the directive plane) throughout its entire length (Fig. 10). The angle between the directive plane and the commissural plane is termed the angle of incidence. While the directive plane describes a planospiral (i.e. the directive spiral) all other radial elements are effectively turbinate spirals. The demarcation line and the directive spiral coincide only in symmetrical equivalve shells like *Pecten* or *Glycymeris*. Knowing the angles of incidence, the angle of the directive spiral, and the shape of the generating curve (which he obtained graphically), Lison could effectively describe the form of any bivalve shell in mathematical terms. The angle of incidence also influences other shell features such as the development of the lunule and escutcheon and the position of the umbones (Cox 1969). Carter (1967a) considers that Lison's often criticized and neglected work represents a major contribution to the understanding of bivalve shell form and has not been accorded the attention which it obviously deserves.

Raup (1966) examined the influence of four different parameters on shell growth: (1) the shape of the generating curve (S); (2) the distance between the generating curve and the axis of coiling (D); (3) the rate of whorl expansion (W); and (4) the degree of whorl translation (T), i.e. the rate at which the whorl moves down the y axis. By altering each of these parameters except (S), Raup produced a broad array of computer generated cones (Fig. 11). He noted, however, that only a limited number of architectural designs were ever actually found among bivalves. Most of the geometrical forms that were possible for logarithmic coiled shells were never utilized, suggesting that the evolutionary potential for this particular skeletal structure is perhaps rather restricted. Spiral growth thus seems to impose certain morphogenetic constraints on shell form in bivalves where only a finite number of solutions to particular functional problems appear to be possible (see also Kauffman 1969; Trueman 1964; Vermeij 1970). Most taxa favor compact, rather than peaked, conical shells; flatter laterally compressed valves probably improve the A/V ratios of the adductor muscles and thus their strength and efficiency.

The mantle-shell and the visceral mass have been considered to be separate but interacting entities. This concept of "independent entities" proposed by Yonge (1952, 1953a, 1955) led to the use of a dual system of orientational axes (see Fig. 9). In symmetrical shells like Glycymeris, shell and body axes are parallel but in most bivalves these axes become offset in various ways as the mantle-shell rotates about the fixed visceral mass. Stasek (1963a) criticizes this scheme and maintains that the body and shell are inseparable and evolve as an integrated unit. Comparable regions of the mantle-shell are always adjacent to comparable regions of the body. Differences between bivalves which vary markedly in body form are the result of changes in the relative proportions of the body and shell as a single entity. Stasek thus developed a uniform system of orientational terms and used transformational diagrams like those originally used by Thompson (1942) as a means of emphasizing the evolutionary unity between the mantle-shell and the rest of the body (Fig. 12). While both the concept of "independent entities" and the theory of transformation have led to a better understanding of bivalve growth and form, their use has caused some confusion concerning directional terminology. For example, in razor clams is the region of the shell from which the foot emerges anterior in position or is it ventral because the foot is usually considered ventral?

Various models have thus been proposed for analyzing total body form in bivalve molluscs. Nevertheless, the considerable difficulties inherent in quantifying the complex changes which accompany alteration in body form, have so far proved a major obstacle to their more generalised use. Growth-gradient studies and, perhaps more especially, multivariate techniques (see Blackith and Rayment 1971), in which the complex interdependence of all variables are examined together, go a long way toward providing a more comprehensive approach to the study of changes in total body form. Although multivariate techniques have so far received comparatively little attention in bivalve growth studies (e.g. Brown et al. 1976; Pohlo 1964; Thomas 1975), their use should ultimately supercede the simple allometric equation as a major quantitative technique fcr the explanatory analysis of allometry (Gould 1966). However, the degree of analytical sophistication should always be related to the kinds of questions being asked and, for many practical purposes, bivariate analysis may in fact prove to be all that is required.

VI. FUNCTIONAL MORPHOLOGY

Most biologists would probably agree that all morphology is adaptive in one way or another. Seilacher (1970) proposes a framework for morphological interpretation in which any structure is examined in terms of the interaction of three important, yet quite distinct, influences. Historical: We have already seen, for example, how the presence of an immutable accretionary skeleton can impose certain mechanical constraints on shell form. Such historical factors constitute the phylogenetic heritage of any evolving lineage. Furthermore, the functional requirements of bivalves may change during ontogeny and features incorporated into the shell at one stage in development may limit subsequent morphological options; adult shells may therefore represent a compromise between different selective forces operating at different times throughout ontogeny. Functional: These factors influence those features of morphology which arise directly from adaptation through natural selection. However, as the response of any one character can potentially influence the functional efficiency of other characters, it is important that all responses to selection pressure should be harmoniously integrated and suitably adapted to the particular life style of the individual. Structural: These factors affect those morphological features which are determined by the inherent nature of the available materials and which need not in themselves necessarily be adaptive. Raup (1972) suggests that two additional factors need to be considered: chance and ecophenotypic effects, the latter being of particular interest within the context of this book. The importance of chance factors should not be underestimated because any specific functional problem may have several possible solutions and whichever solution is adopted need not necessarily be the outcome of selection; the observed morphology may, in fact, be the best one possible within the constraints imposed by the nature of the materials. Ecophenotypic factors determine the extent of phenotypic variation that is possible within any given genotype. Although such phenotypes could be considered functionally advantageous, this is not invariably the case. Densely crowded mussels, for example, develop elongate shells, yet such growth forms are probably functionally inferior to the taller more expanded shells which develop in non-crowded conditions. The interpretation of any morphological feature therefore depends on the relative contribution made by each of the above factors (Fig. 13). While bivalve morphology is thus ultimately controlled by several distinct factors, most work to date has concentrated upon the functional (= adaptive) significance of particular morphologies and the evolutionary processes by which these were produced.

Bivalve molluscs provide excellent material for biologists and paleontologists whose interests lie in aspects of functional morphology. They exhibit extensive adaptive radiation, their shells frequently reflect environmental demands and they have a long and successful evolutionary history, with comparatively few extinctions. Furthermore, convergence and divergence both between and within members of phylogenetically distant taxa has led to considerable homeomorphy (Stanley 1970; 1975a). This is especially well-illustrated among the Mactracea (Fig. 14). Although homeomorphy presents difficulties in recognizing major phylogenetic relationships within the Bivalvia, it does provide strong evidence for the adaptive significance of shell morphology. Detailed studies of functional morphology have been made on a number of diverse bivalve taxa e.g. Veneracea (Ansell 1961; Carriker 1961; Pohlo 1964; Purchon 1955; Sellmer 1967), Arcacea (Thomas 1976; 1978), Carditacea (Yonge 1969), Astartacea (Allen 1968; Saleuddin 1965), Lucinacea (Allen 1958; Kauffman 1969), Mytilacea (Yonge 1955), Tellinacea (Wade 1969; Yonge 1949), Chamacea (Yonge 1967), Pandoracea (Allen and Allen 1955), Nuculacea (Yonge 1939), Cyprinacea (Saleuddin 1964), Pholadacea (Purchon 1955), and Erycinacea (Oldfield 1955; Morton 1973). In addition to work on selected taxa, several excellent comparative studies of form, function, and evolution within the Bivalvia are also available (e.g. Allen 1963; Eager 1978; Kauffman 1969; Stanley 1968; 1970; 1972; 1975a). Attention has already been drawn to the two major evolutionary events in bivalve evolution: adult retention of the byssus, and siphon development. We shall conclude this chapter by briefly considering the impact that these two important events have had on bivalve shell morphology.

Bivalve shell shape is remarkably plastic and similar life styles in many unrelated lineages reveal numerous instances of parallel or convergent evolution. Consequently, it has generally been considered appropriate to group bivalves according to life styles and habitat preferences (e.g. Kauffman 1969; Kranz 1974; Purchon 1977; Schafer 1972; Stanley 1968; 1970). Although several environmental factors are undoubtedly important in controlling shell morphology (Fig. 15), water movement, via its effects on food supply and on the nature of the substratum, is arguably the most important single factor (Stanley 1970).

Byssal attachment is widespread among many exceedingly diverse groups of bivalves (Table 1). Many of the shell features associated with epibyssal attachment to hard substrata can be considered as adaptations for improving physical stability. Epibyssate taxa like mussels, where the commissure plane is vertical, are usually anisomyarian with elongate, equivalve shells. Maximum shell width is situated close to the ventral shell margin, thereby lowering the center of gravity and providing a broad base for fixation (Stanley 1972). Seed (1968) found that in Mytilus many of these shell features which enhance physical stability become more pronounced in older individuals, strongly suggesting that they do indeed have adaptive value. The wedge-shaped profile of these anisomyarian shells effectively elevates the posterior current flow and may be beneficial to animals living in densely crowded conditions (Yonge and Campbell 1968). Stasek (1966) considers that posterior expansion associated with the anisomyarian condition may, in fact, have evolved in the tropics as a method for improving feeding efficiency in comparatively nutrient poor waters. The development of a powerful posterior adductor muscle places considerable strain on the ligament, and the small anterior adductor muscle is retained in order to prevent the ligament from splitting. Arc shells (Arcacea), which are among the least modified of byssally attached bivalves, have probably been compelled to retain the primitive isomyarian condition by virtue of their exceedingly weak ligament (Thomas 1976).

Stanley (1972) suggests that a transitional period of infaunal or semifaunal byssal attachment probably preceeded the ultimate colonization of hard substrata. Although originally abundant, these endobyssate bivalves gradually declined with the appearance of epifaunal and free burrowing forms and they now persist only in a few Recent taxa such as *Modiolus* and *Brachidontes* (see also Thayer 1979). The lineage from *Modiolus* to *Mytilus* represents a gradual transition from an endobyssate to an epibyssate way of life (Stanley 1972). The adaptations accompanying this transition are illustrated in Figure 16 and include a gradual reduction of the anterior region of the shell, the development of a steeper hinge angle, a strengthening and change in position of the byssal retractor muscle in order to pull the shell down more firmly against the substratum, and a change in cross sectional shape. Many of these features are even more pronounced in *Mytilus galloprivincialis* than they are in *M. edulis* (Seed 1978), supporting the belief that *M. galloprovincialis* is probably of comparatively recent origin, having evolved in the warmer, enclosed waters of the Mediterranean. Taxa which are byssally attached in a non-vertical position tend to be inequivalve because physical conditions on the two valves may vary quite considerably. A recurrent stabilizing strategy among these taxa is the development of shells with two marginal points of contact with the substratum, one on either side of the byssal sinus (this is also encountered in some mytilids when the ventral margin appears incurved in lateral view). In the Pteriacea and Pectinacea this is generally achieved by means of an elongate anterior auricle (see Fig. 17). Jingle shells (Anomiacea) are exceptional among byssate taxa in that the byssus forms a calcified plug which passes through an embayment in the flat lower valve. They are exceedingly variable in shape, thickness and sculpturing, often closely following the contours of the substratum to which they are attached (Seed and Roberts 1976). Cementation which occurs, for example, in oysters (Ostreacea) is more commonly encountered in warmer waters where carbonate is more easily deposited (Nicol 1964). Cemented bivalves typically have thick, well-ornamented shells for protection against predators. Taxa which recline freely on the surface of the sediment improve their physical stability by increasing bulk density. They may also have a convex lower valve in order to raise the commissure above the sediment surface and thus prevent clogging by suspended particles. Swimming, by clapping the valves together, has evolved among scallops and file shells (Pectinacea), probably from a mechanism originally designed for cleansing the mantle cavity of pseudofeces (Yonge 1936). Scallops from high energy environments are typically more heavily ribbed than the proficient smooth shelled swimmers from deeper, less turbulent, waters. Whereas byssally attached pectinids are rather asymmetrical, swimming taxa have broad, lightweight shells with a large umbonal angle (Fig. 17). Bivalves which nestle in crevices are generally irregular in shape due to their confined environment.

Most bivalve taxa are infaunal burrowers in which life habit, and therefore shell morphology, is determined principally by the nature of the substratum. Burrowing mechanisms are reviewed by Trueman (1966; 1975). Most advanced taxa (except the Lucinacea) orient themselves with posterior siphons uppermost and the hydraulic foot, which emerges more or less parallel to the long axis, directed forward and downward into the substratum. Unlike bysally attached bivalves, most burrowing taxa retain the primitive isomyarian condition. Maximum shell width, which in epibyssate forms was located near the ventral shell margin, is here moved dorsally, thus leaving a knife-like leading edge to the shell for more efficient burrowing. Clam-shaped shells, which are more or less circular in lateral view (i.e. with low length/height ratios), burrow by means of a series of anterior-posterior rocking movements brought about by alternate contraction of the anterior and posterior adductor muscles. Stanley (1975b) simulated these burrowing movements experimentally using plaster casts of shells and showed that the prosogyrous shape and flat lunule were advantageous design features. Such shell rotations would obviously be impossible in elongate taxa like razor shells in which the foot emerges from an anterior pedal gape. Here penetration of the substratum occurs almost parallel to the long axis via the piston-like action of the foot within the elongate cylindrical shell. Stanley (1970) compared burrowing efficiency in several infaunal bivalves by means of the burrowing rate index (b. r. i.) where:

$$\text{b.r.i.} = \sqrt[3]{\frac{\text{mass (g)} \times 100}{\text{burrowing time}}}$$

For any given species this index does not change appreciably during ontogeny and it therefore remains independent of size. Most rapid burrowers were found to have streamlined shells which were either disc-like, blade-like, or cylindrical in shape rather than globular (Fig. 18a). Many carditids, however, are exceptionally good burrowers, but this is due to a powerful foot rather than to their obese shape. Thick and/or highly ornamented shells hinder burrowing (Fig. 18b) although radial ribbing and divaricate (zigzag) ornamentation can sometimes be an asset, especially in taxa with more globular shells where it offsets the disadvantages of shape. Shallow sand burrowers, which are subject to frequent disinterment, generally have thick shells, often with pronounced ribs or ridges for additional protection and stabilization. Radial ribbing also permits the valve edges to interdigitate and thus prevents lateral shearing; fine denticulations on the inner edges of the valves of certain bivalves (e.g. *Donax*) serve the same function. In shallow burrowing arcids and carditids, the broad, flat posterior shell region lies parallel to and immediately beneath the sediment surface. Deep burrowers, by contrast, obtain substantial protection from the sediment itself and tend, therefore, to have thinner non-ornamented shells. Many species (e.g. *Mya*) may lose the ability to burrow as adults once their required depth has been attained. Because they are not faced with problems of shear, many deep burrowing taxa have more concentrated ligaments, while hinge teeth may be reduced or even absent. This allows the valves to rock about the dorsal-ventral axis, a movement which, together with a posterior gape is necessary for the efficient accommodation of the elongate fleshy siphons. Vermeij and Veil (1978) found that infaunal bivalves with permanent posterior gapes become increasingly rare towards the tropics and attributed this to enhanced predation. Such latitudinal trends in predation and bivalve architecture (tropical taxa also have thicker, more highly ornamented shells) are therefore broadly in keeping with the parallel reduction in the proportion of gaping taxa from deep to shallow sediments. Carter (1968) reviews some of the strategies used by bivalves to avoid predation. Tellinids are unusual among burrowing infaunal taxa in that their thin, sometimes inequivalve shells lie horizontally in the sediment. Holme (1961b) suggests that this probably facilitates horizontal migration, so important to deposit feeders which rapidly deplete their local food supplies. Coarse shifting deposits of high energy habitats, where disinterment is a recurring hazard, are colonized only by active burrowers. Many taxa like *Tivela* and *Donax* may even develop comparatively thick shells for improved stability and protection even though these features may slightly impair burrowing efficiency. Soft, muddy deposits more typical of bays and estuaries are rich in organic material and are largely dominated by deposit feeders (Tellinacea, Nuculacea). The turbidity associated with physically unstable, fine-grained sediments, however, is detrimental to suspension feeders and these taxa are therefore largely excluded from such habitats (Rhoads and Young 1970). Mud dwelling taxa have small, thin shells in order to reduce their bulk density and thereby prevent themselves from sinking too deeply into the soft sediment. These deposit feeders are mainly active, streamlined burrowers which rapidly exhaust their local food supplies. Bioturbation, caused by the burrowing activity of deposit feeders, may also be an important means of enhancing microbial turnover rates; this is mediated by the control of sediment chemistry through the bioturbation process (Rhoads, McCall and Yingst 1978). By contrast, more cohesive sediments consisting of stable sandy mud are rich in suspension feeding bivalves. Kranz (1974) demonstrated that certain features of shell morphology correlated well with the ability of bivalves to escape burial by sediment (e.g. anterio-ventral expansion indicates a relatively large foot and therefore good escape potential). Moreover, because these escape responses could be shown to be influenced by several environmental factors, bivalves are potentially excellent indicators of sedimentary regimes. Boring into hard substrata, such as rock or wood, is an extremely specialized life style (e.g. Nair and Ansell 1968; Purchon 1955; 1956a,b; Turner 1966; Yonge 1955). Penetration may be accomplished mechanically (e.g. *Botula*, *Hiatella*) or chemically (e.g. *Lithophaga*), and the substratum may even be utilized as food (e.g. *Teredo*). The shells of boring taxa are often reduced and function merely as efficient cutting tools: accessory shell plates may also be developed. A condensed ligament which provides a flexible joint around which the two valves can rock about the dorsal-ventral axis has been instrumental in the evolution of an effective boring mechanism.

We have seen, therefore, that the bivalve shell is subject to considerable phenotypic expression. Critical evaluation of such variation both during ontogeny and with respect to changing environmental conditions, provides valuable information regarding the functional significance of various morphological features. Moreover, many of these features, such as overall shell proportions, cross-sectional shape, muscle scars, the presence of gapes and sinuses, or the ligament type are frequently well preserved in fossil material and thus provide the paleontologist with a potentially valuable tool in paleoecological interpretation. Considerable progress in the study of functional morphology has been made over recent years. Further detailed research in this field should ultimately lead to an even better understanding of bivalve evolution and to the establishment of a more acceptable framework for interpreting the fossil record.

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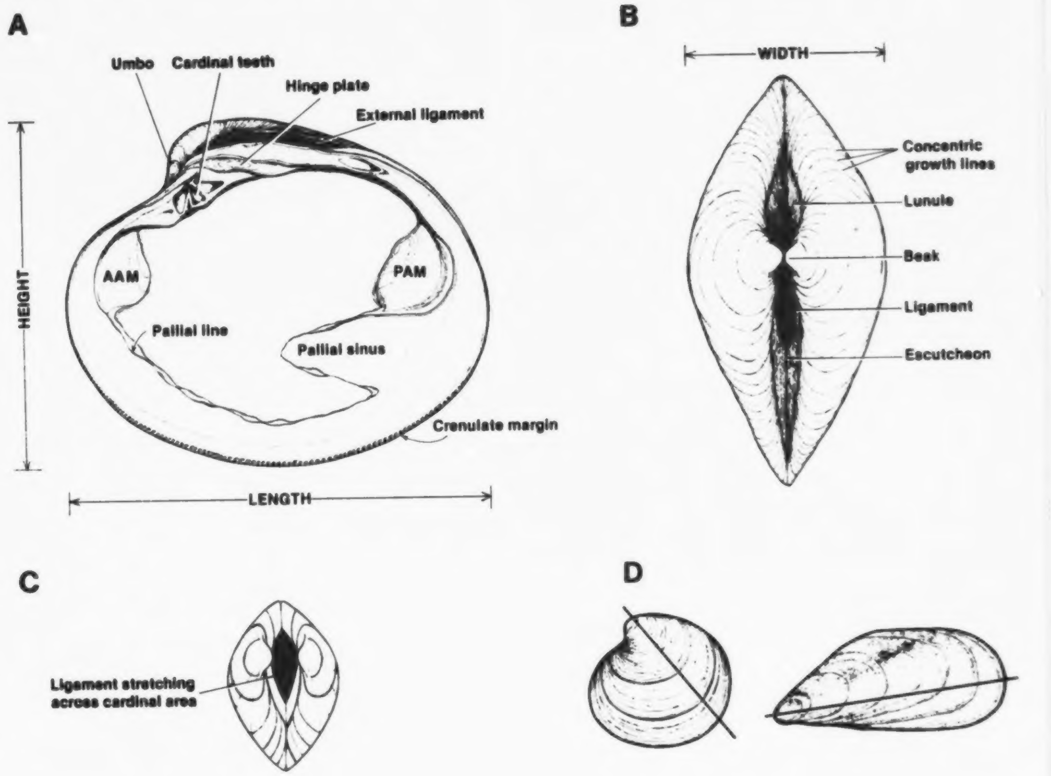

Figure 1A. Generalized bivalve illustrating the structure and terminology of the shell. (A) Inside of right valve. A.A.M and P.A.M. = anterior and posterior adductor muscle scars respectively. (B) Dorsal view of shell. (C) Dorsal view of shell with extensive cardinal region. (D) Axis of maximum growth in a clam (left) and a mussel (right).

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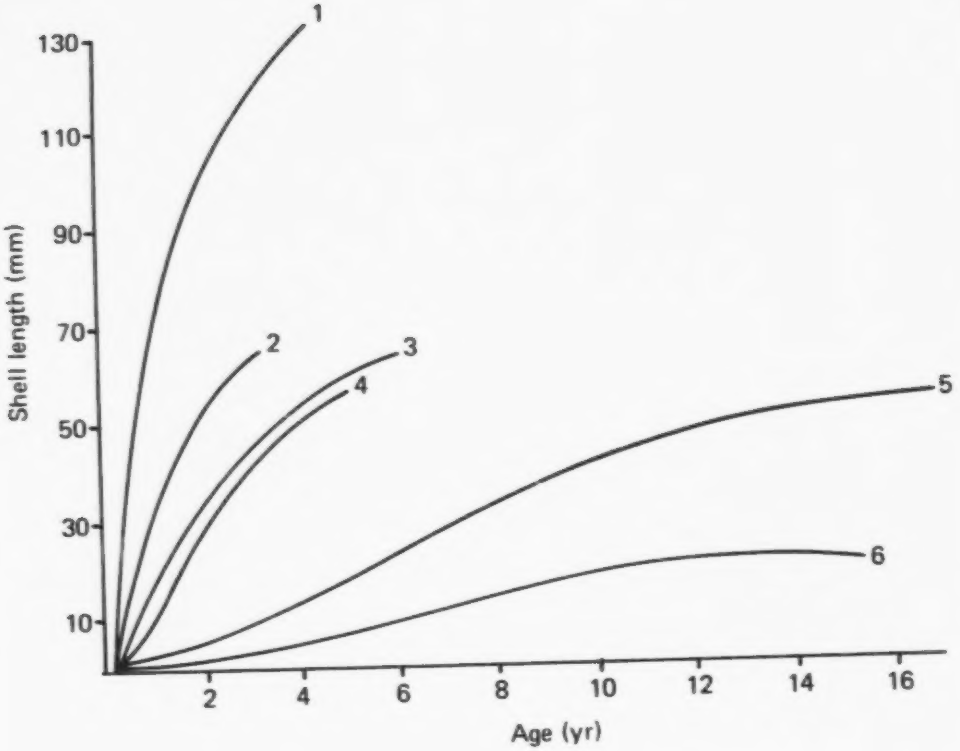

Figure 2. Growth curves for six populations of Mytilus. (1) *Mytilus californianus* (subtidal); (2) *Mytilus edulis*, River Boyne (subtidal); (3) *Mytilus edulis*, Chichester Harbour; (4) *Mytilus edulis*, Conway (subtidal); (5) *Mytilus edulis*, Filey Bay (high-shore); (6) *Mytilus edulis*, Robin Hood's Bay (high-shore). (After Seed 1976).

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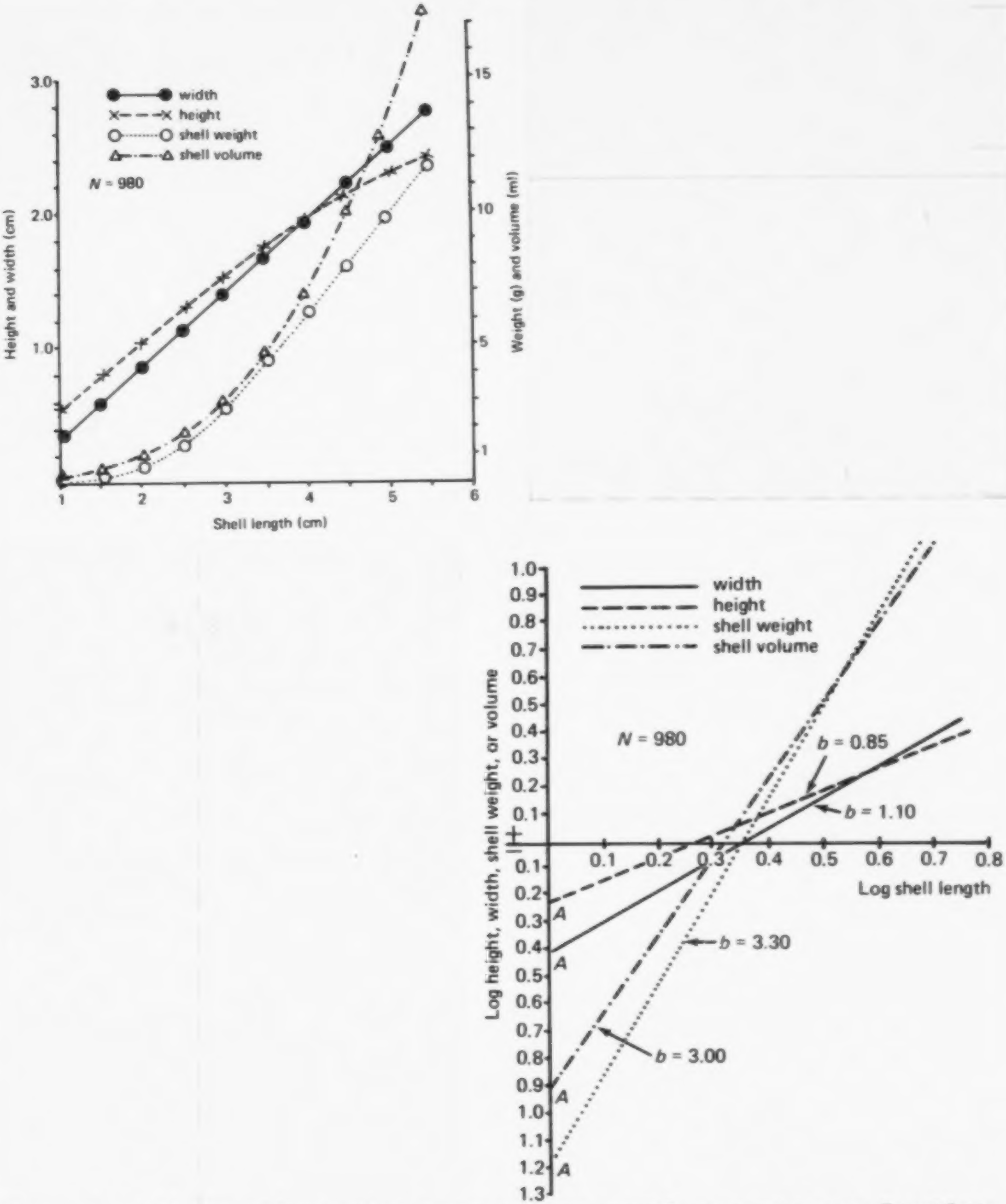

Figure 3. (A) The relationship among various growth parameters as functions of shell length for a high-shore population of *Mytilus edulis* (Filey Bay, northeast coast of England); (——) width; (- - -) height; (· · · ·) shell weight; (·-·-·) volume. (After Seed 1973). (B) Log transformation of data presented in (A). (A) = Y-intercept; (b) = slope.

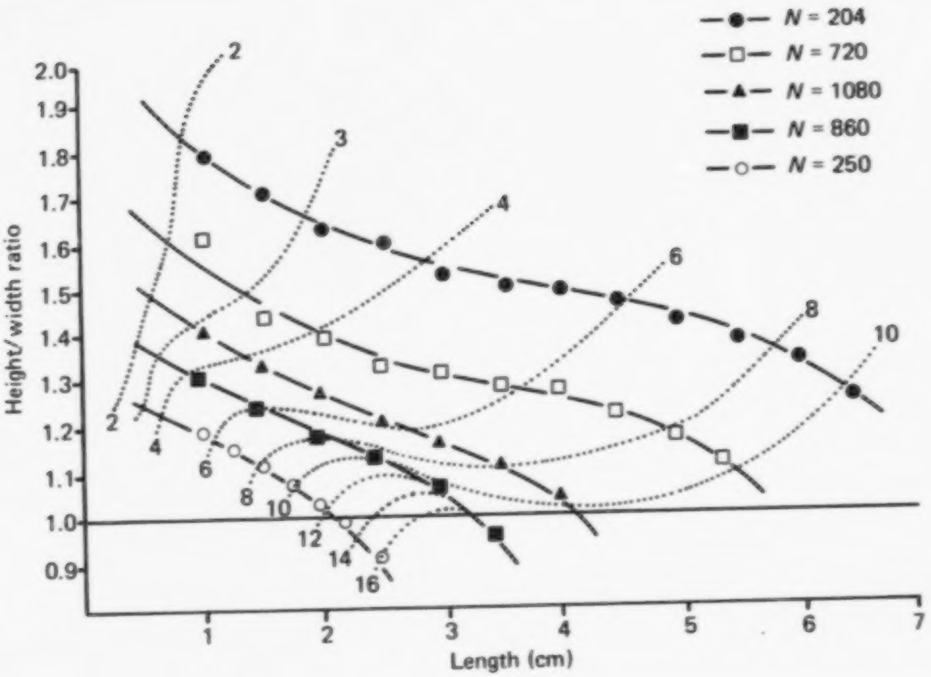

Figure 4. The relationship between height/width ratios and shell length in several populations of *Mytilus edulis*. —— Whitby Harbour (M.L.W.S.); —— Filey Bay (low-shore); —— Filey Brigg (mid-shore); —— Filey Brigg (high-shore); —— Robin Hood's Bay (high-shore). Age contours (yrs). Whitby Harbour and Filey Bay are low-energy environments, while Filey Brigg and Robin Hood's Bay are high-energy environments. (After Seed 1968.)

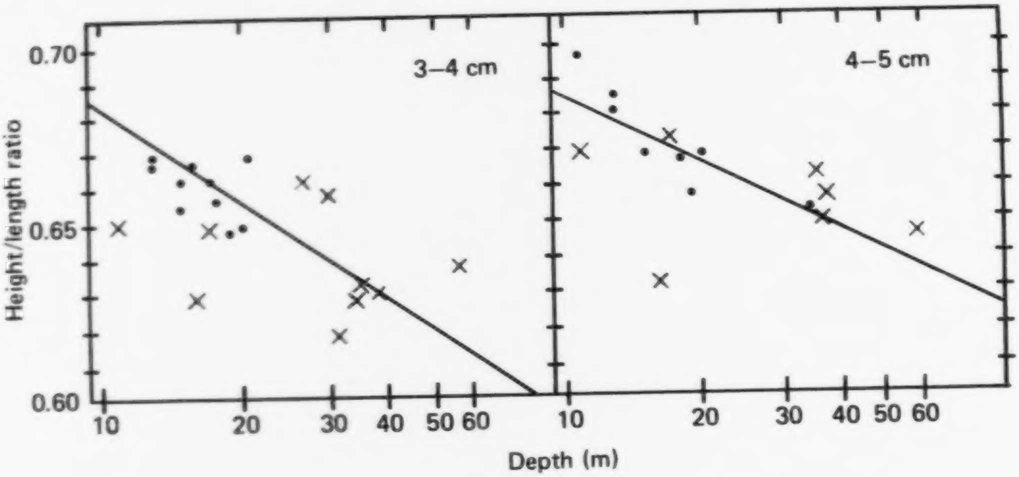

Figure 5. Regressions of median height/length (H/–) ratios of *Venerupis rhomboides* on water depth. Samples from muddy sediments: (0); samples from "clean" sediments: (X). Ratios for 3-4 and 4-5 cm length groups are plotted separately, as some change in proportions occurs with increasing length. (After Holme 1961.)

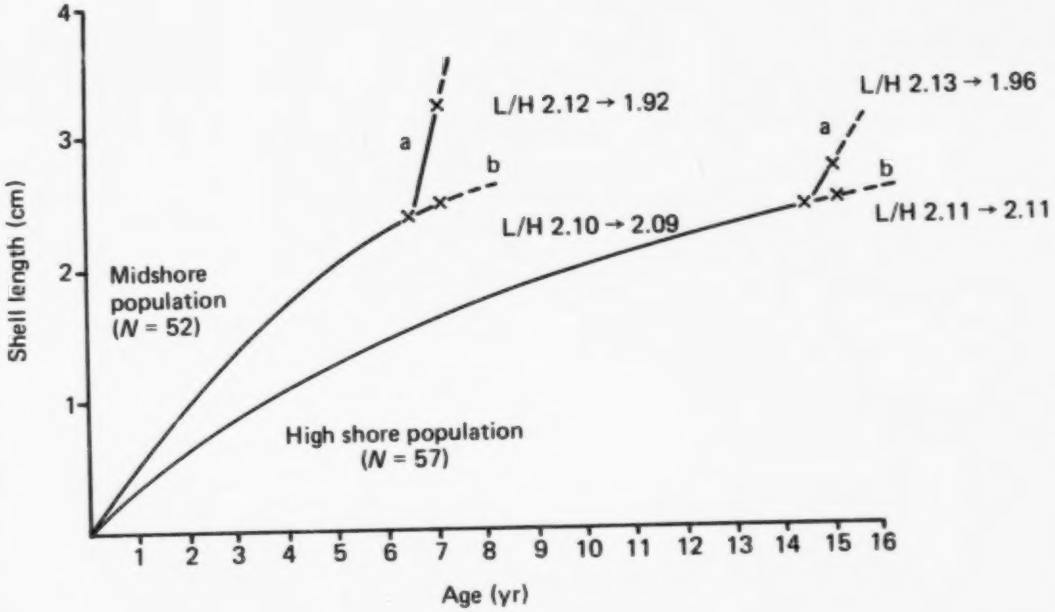

Figure 6. Changes in length/height (L/H) ratios and growth rate over one growing season in two exposed shore populations of Mytilus edulis after transplantation to cages at low intertidal levels in a sheltered estuary (Whitby Harbour, northeast coast of England). (a) = experimental animals; (b) = controls. (After Seed 1978.)

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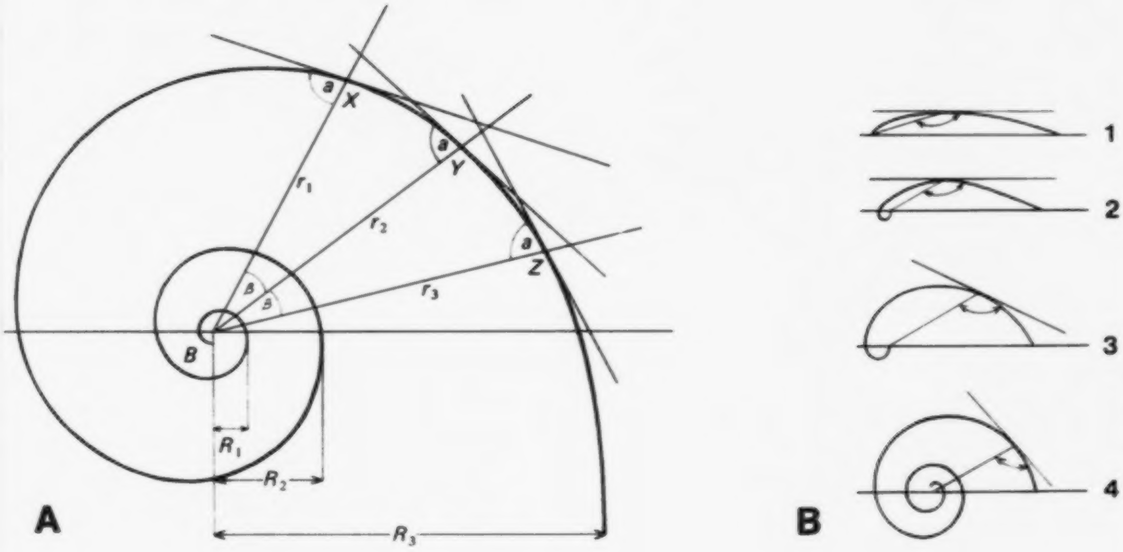

Figure 7. Bivalve shell geometry; properties of the logarithmic or equiangular spiral. (A) Triangles BXY and BYZ, in which the angle at B (β) is the same, are always similar. Angle (a) formed between tangents and raii (r_1, r_2, r_3) is always constant. (B) Sections through beak and front edge of shell showing correlation between decrease in angle of equiangular spiral and increase of shell convexity. (After Cox 1969; and Lison 1949.)

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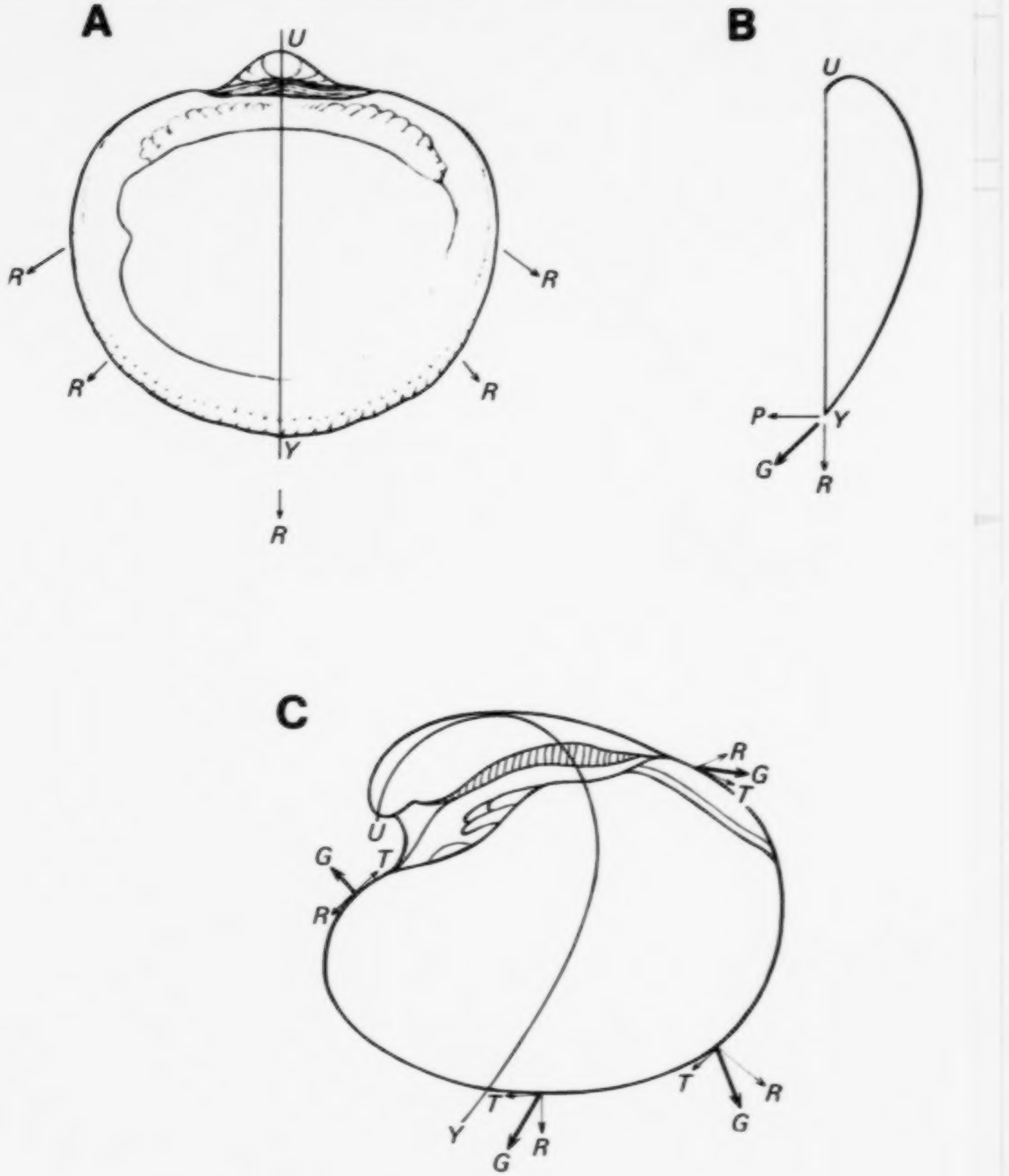

Figure 8. Growth vectors of the bivalve shell. (A) Left valve of *Glycymeris* sp. (B) Section of (A) through UY. (C) Left vale of *Glossus* sp. (G) = direction of growth at shell margin; (P) = transverse component; (R) = radial component; (T) = tangential component; (UY) = demarcation line or normal axis. (After Owen 1953.)

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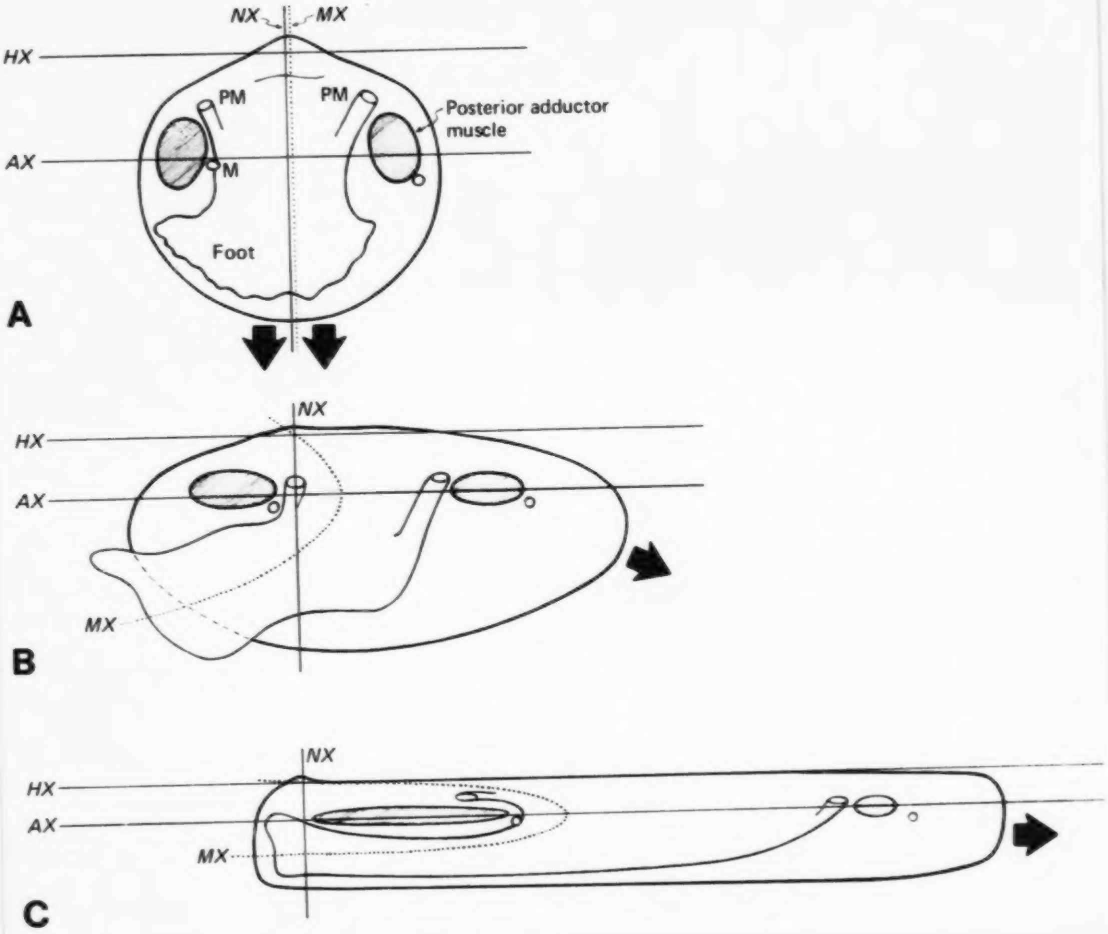

Figure 9. Distortion of Ensis sp. (C) and Siliqua sp. (B) relative to Glycymeris sp. (A) according to the concept of independent entities. Stoll axes: (NX) = demarcation line (or normal axis); and (HX) = hinge axis. Body axes are: (AX) = antero-posterior axis; and (MX) = median axis. (M) = mouth; (A) = anus; (PM) = pedal muscles. Heavy arrows denote direction of maximum growth. (After Yonge 1952.)

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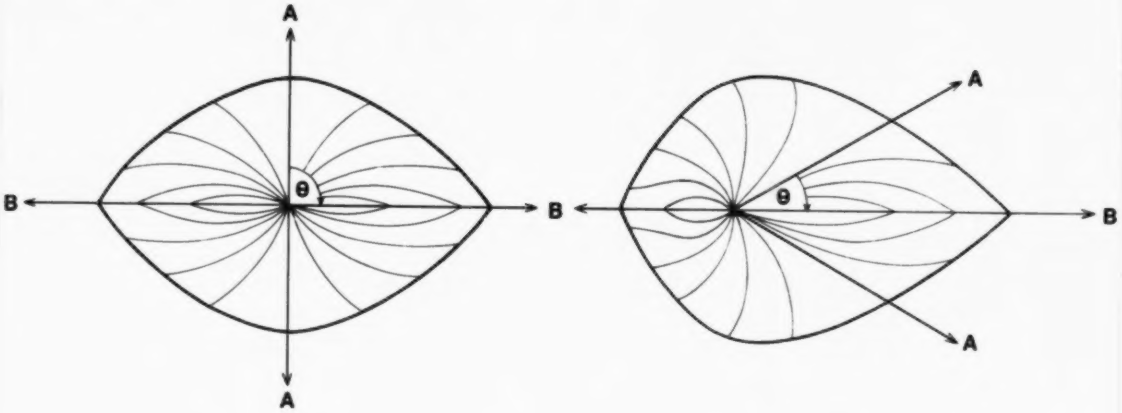

Figure 10. Bivalve shell geometry; shells viewed dorsally. The directive plane (A) and the plane of commissure (B) are indicated by arrows. The angle between these planes (θ) defines the angle of incidence. (After Owen 1953.)

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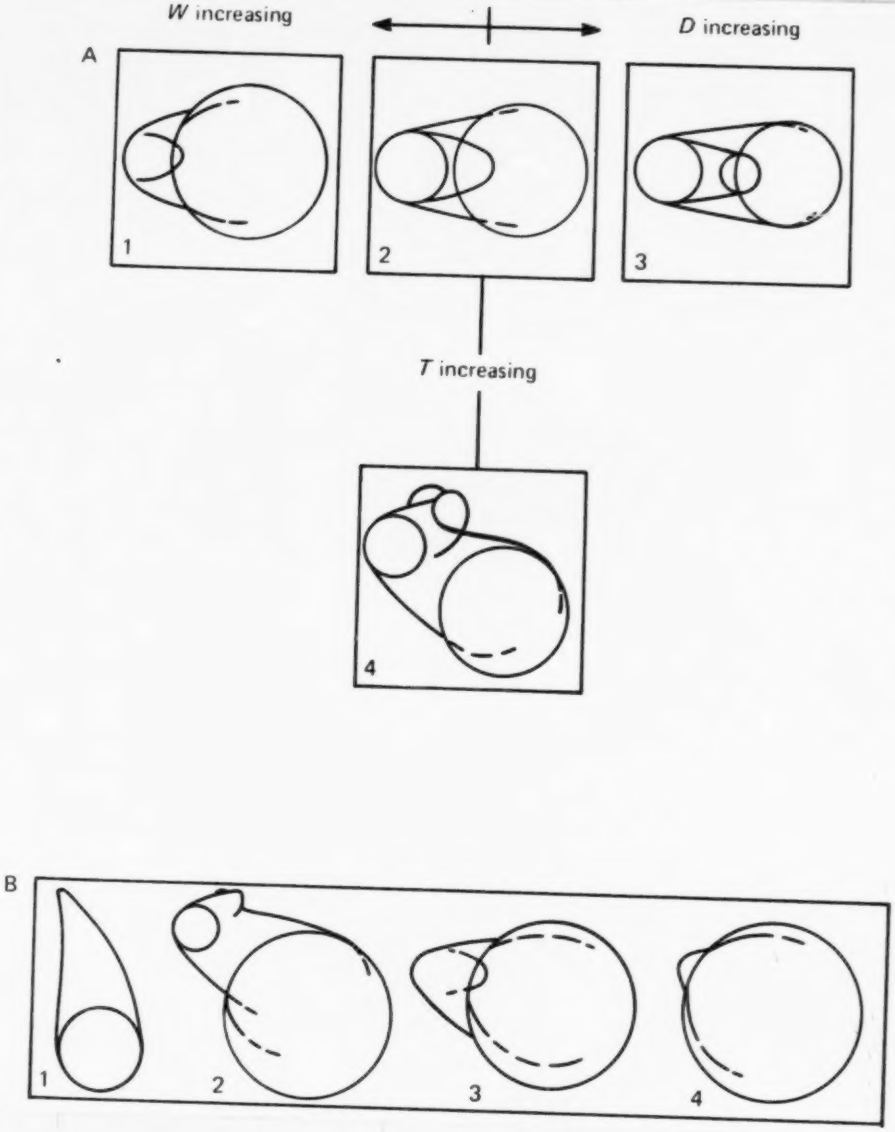

Figure 11. Bivalve shell geometry; parameters and models of shell form in molluscs. (A) Explanation of parameters used in construction of theoretical shell forms. The generating curve in all cases is circular. (1) A_1 - typical planispiral gastropod; (2) A_2 - bellerophontid gastropod; (3) A_3 - evolute ammonoid; (4) A_4 - spired gastropod. (B) Models of shell form found in Bivalvia. (1) B_1 - typical rudist with high whorl expansion (W) and high whorl translation (T); (2) B_2 - *Diceras* sp. with relatively low W and intermediate T; (3) B_3 - *Gryphaea* sp. with relatively low W and low T; (4) B_4 - slightly equilateral shell of typical form with high W and low T. (After Cox 1969 and Raup 1966.)

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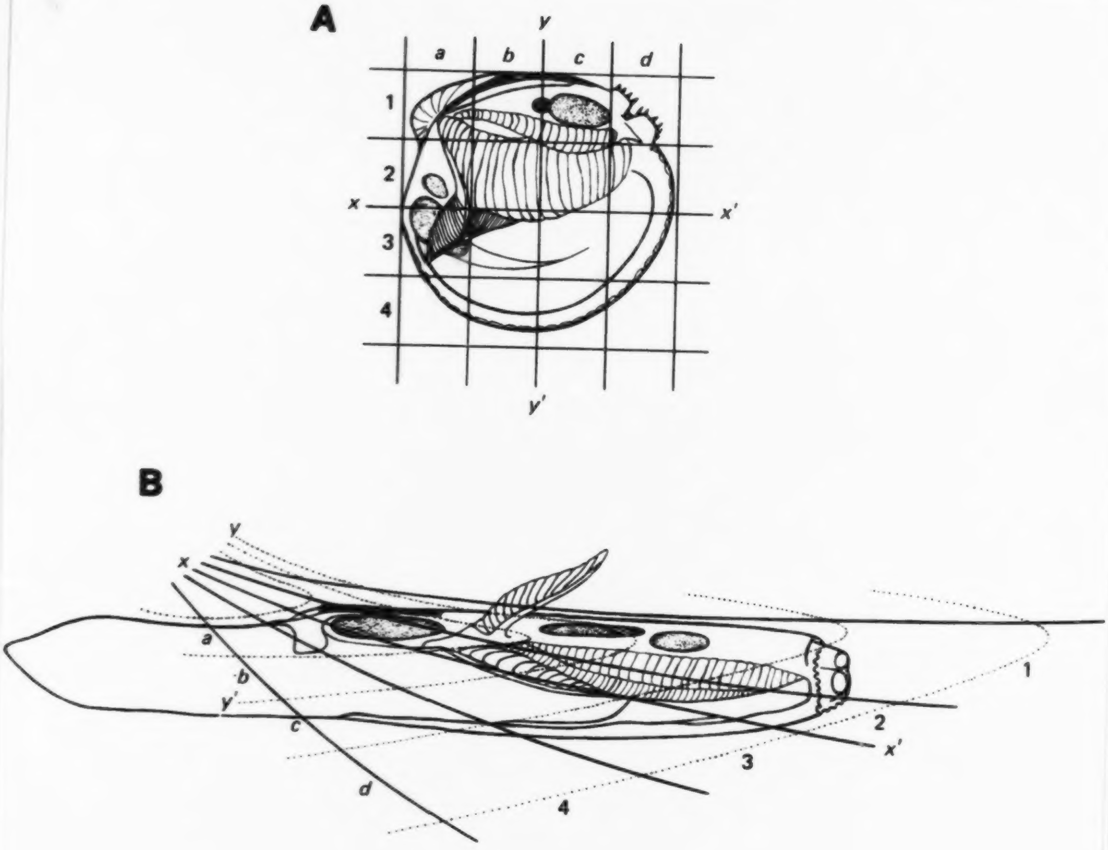

Figure 12. Deformation of Solen sp. (B) relative to Clinocardium sp. (A) using coordinate transformation. (After Stasek 1963.)

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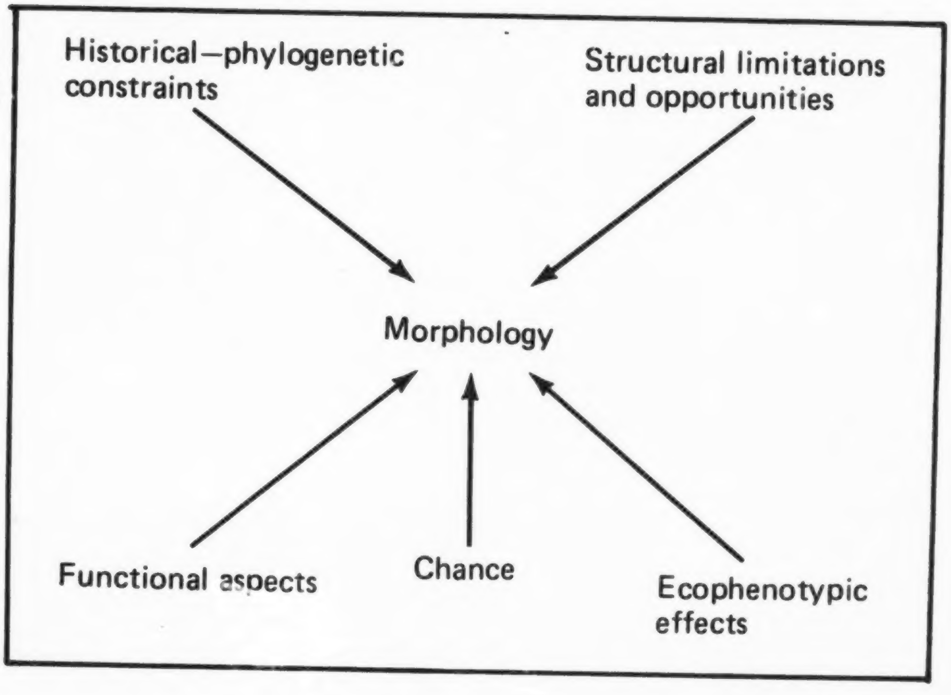
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Chance
Ecophenotypic effects

Figure 13. Principal factors controlling shell morphology. (After Raup 1972.)

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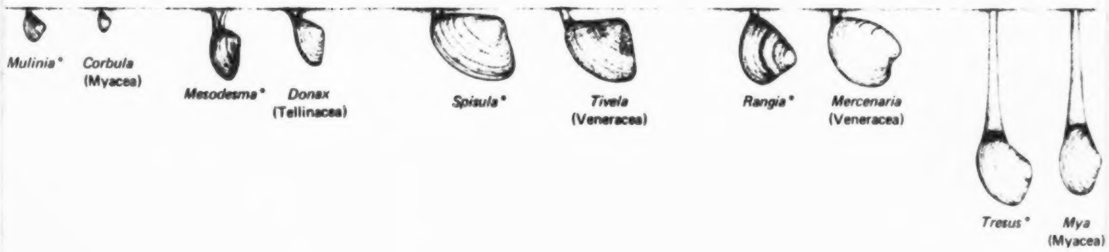

Figure 14. Adaptive divergence of the Mactracea and convergence in form and habit with unrelated burrowing taxa. (After Stanley 1970.)

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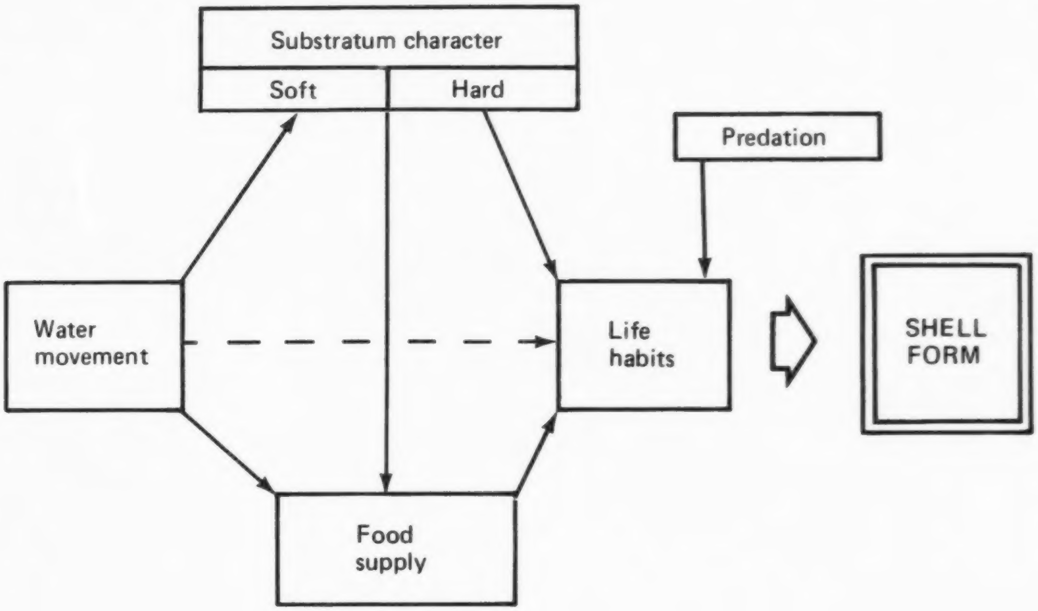

Figure 15. Interrelationships among environmental factors and bivalve life habits. Solid lines indicate major effects; dotted line, minor effects. (After Stanley 1970.)

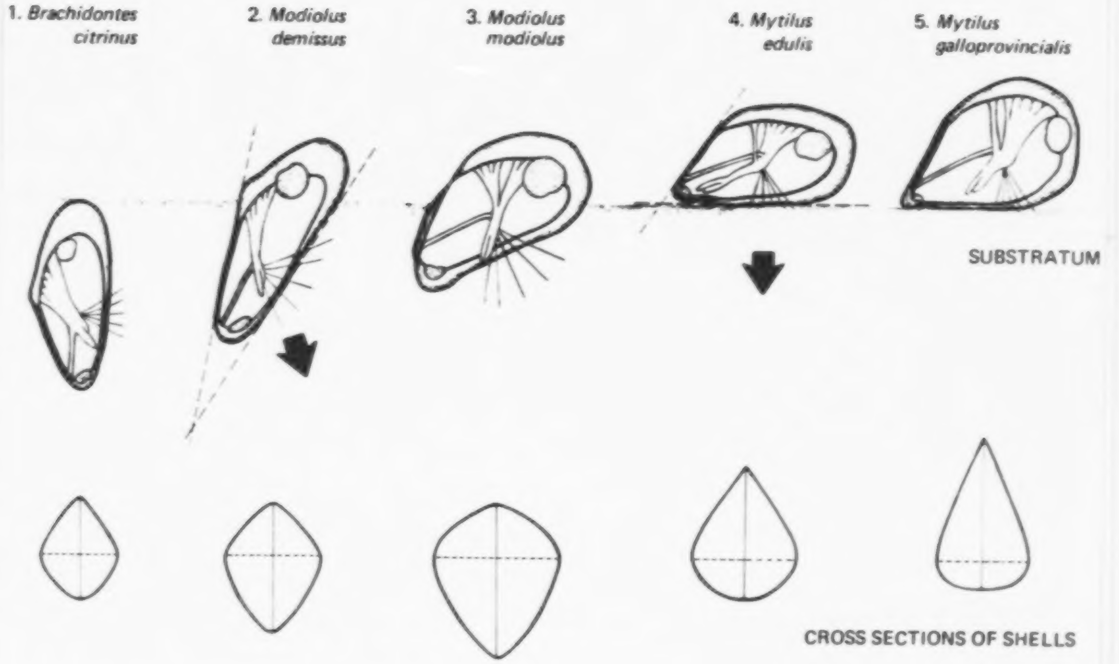

Figure 16. Grades of evolution in Recent Mytilidae. Heavy arrows in (2) and (4) indicate the direction and relative force of the shell against the substratum. Small arrows indicate the regions of maximum shell width. Striped regions designate portions of the shell that are ventral to the point of maximum width. (After Stanley 1972 and Seed 1978.)

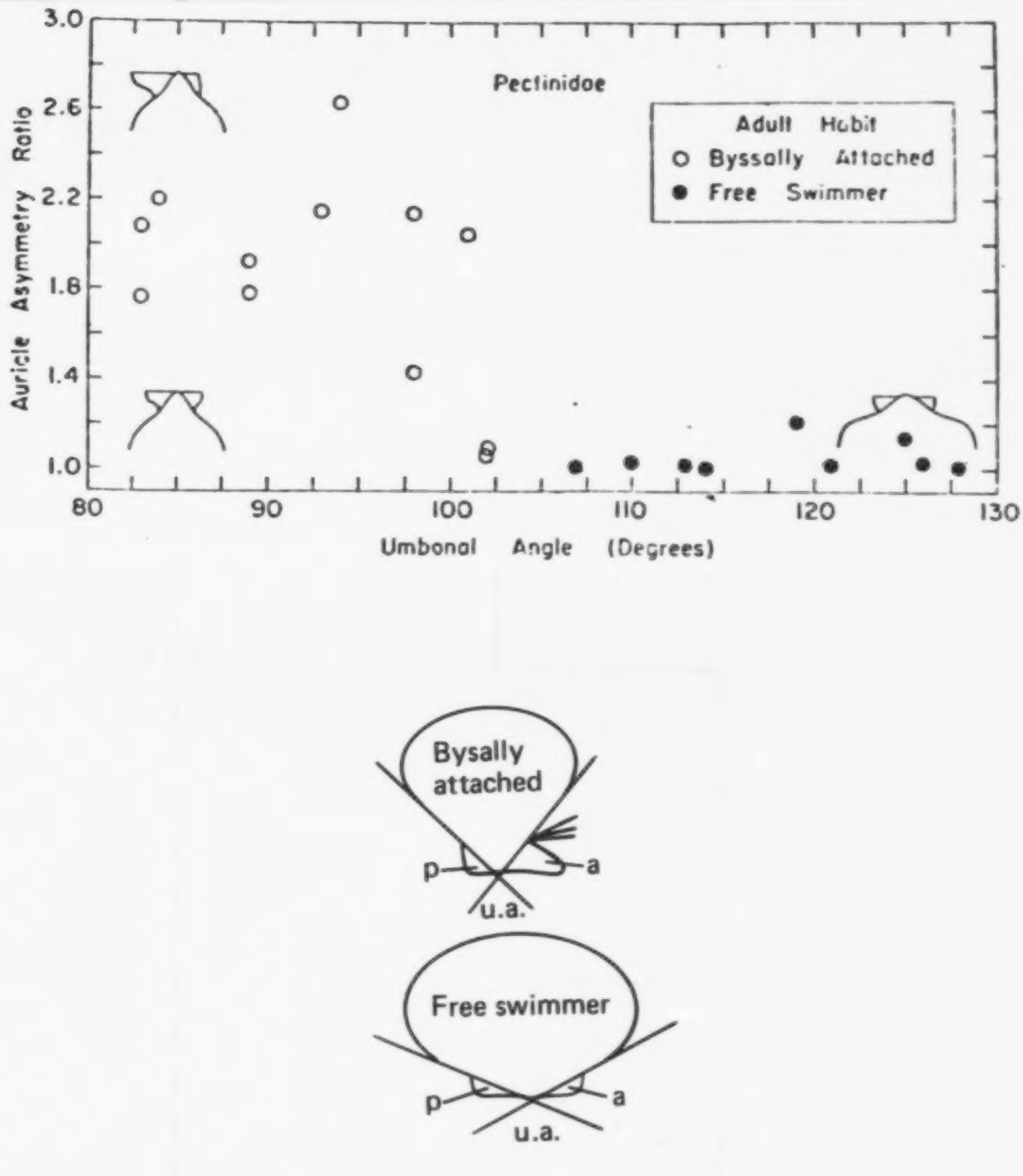

Figure 17. Graph of auricle asymmetry *versus* umbonal angle (*UA*) for byssally attached and free-swimming members of the Pectinidae. The auricle asymmetry ratio is the ratio between anterior (a) and posterior (p) auricle lengths. (After Stanley 1970.)

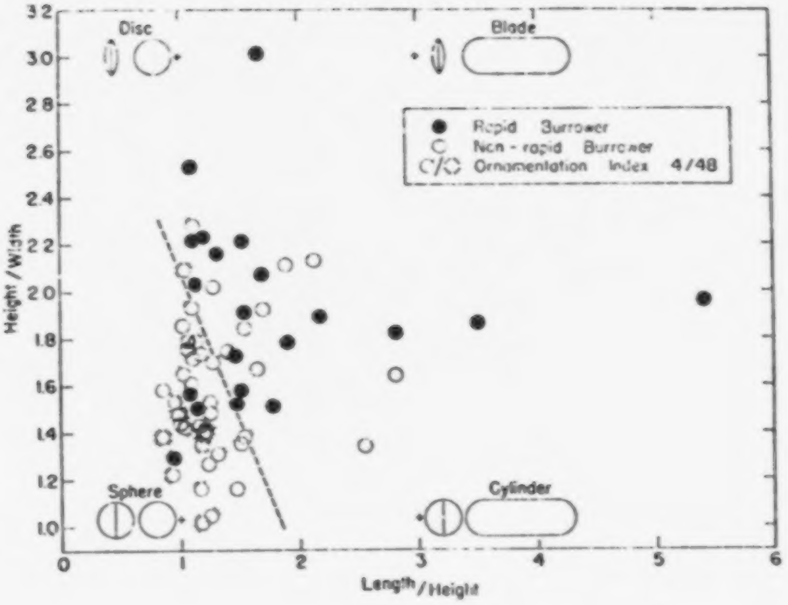

Figure 18. (a) (A) Relationship of burrowing rate to gross shell shape and shell ornamentation. Empirical dashed line separates rapid-burrowing region from slow-burrowing region. (B) Relationship of burrowing rate to shell thickness, shell ornamentation, feeding type, and substratum character. From these data one may draw the following conclusions:

(1) Nearly all (19 of 22) thick-shelled species are slow burrowers.

(2) Nearly all (18 of 21) rapid burrowers have very thin to moderately thick shells.

(3) Nearly all (19 of 21) rapid burrowers are either (a) deposit feeders, or (b) inhabitants of moderately unstable shifting substrata.

(4) Only 1 of 16 deposit feeders is a slow burrower.

(5) Nearly all (12 of 13) species with moderately coarse or very coarse ornamentation are slow burrowers. (After Stanley 1970.)

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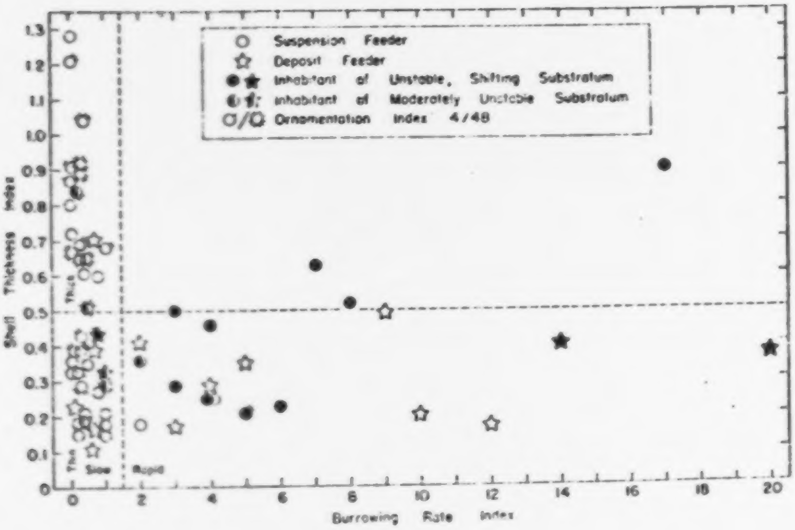

Figure 18(b).

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Table 1. Distribution of Marine Bivalve Genera Among Major Life Habit Categories.

		Method of Attachment or Locomotion	General Life Position		
			Epifaunal	Semi Infaunal	Infaunal
Substratum Type	Soft Substrata	Reclining	1	1	———
		Burrowing	———	(1)	166(3)
		Byssally Attached	21(4)	3(1)	(3)
	Hard Substrata	Boring	———	———	17(1)
		Nestling	———	———	7
		Cemented	5	———	———
		Swimming	3(2)	———	———

From Stanley (1970).

Parentheses indicate partial representation.

Table 2. Some Values for L_∞ (Maximum Attainable Length) and k (Growth Rate)(Constants in the von Bertalanffy Growth Equation) for *Mytilus edulis*.

Locality	L_∞	k	Authority	Comments
Danish Wadden Sea	77.60	0.5611	Thiesen (1968)	Mussels at low-water spring tides
Conway, North Wales	72.71	0.3426	Thiesen (1968) based on data in Savage (1956)	'Bank mussels'
	74.44	0.3927		'Channel mussels'
Greenland	77.5-283.9	0.022-0.162	Thiesen (1973)	Mussels from 12 very varied sites
Menai Straits, North Wales	67.20	1.1378	G. Davies and P.J. Dare (personal communication)	Mussels suspended on ropes from rafts
Morecambe Bay, England	62.45	0.8103	Dare (1976)	Mussels near low-water mark of spring tides

From Seed (1976).

Table 3. Coefficients of Allometry[1] for Various Combinations of Size Parameters.

Dependent variable[2]	Independent variable[3]	*Cerastoderma edule*	*Mytilus edulis*	*Modiolus modiolus*
Shell weight	Tissue wet weight	*1.074*	*0.957*	*0.968*
Shell weight	Tissue dry weight	*0.990*	*1.044*	0.924*
Shell weight	Shell width	*3.068*	*3.009*	2.908*
Shell weight	Shell height	3.426*	3.868*	3.216*
Shell weight	Shell length	3.437*	3.300*	2.901
Shell width	Shell height	1.117*	1.286*	1.106*
Shell width	Shell length	1.120*	1.097*	0.998
Shell length	Shell height	*0.997*	1.172*	1.108*

From Brown, *et al*. (1976).

[1] The coefficient of allometry is coefficient b in the equation $y=Ax^b$, calculated as the average of the regression slope of log y on log x and of the regression slope of log x on log y. Figures in italics indicate isometry.

[2] The variable y in the equation $y=Ax^b$.

[3] The variable x in the equation $y=Ax^b$.

*Both regression slopes were significant at $P<0.001$.

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CHAPTER 2

ENVIRONMENTAL EVENTS RECORDED WITHIN THE MOLLUSCAN SHELL

by

Richard A. Lutz and Donald C. Rhoads

Department of Geology and Geophysics
Yale University
New Haven, Connecticut
06520

CHAPTER 2

I. INTRODUCTION

Growth patterns on the external surface of the mulluscan shell (Fig. 1) have long been the subject of both biological and paleontological research [Isely 1913, 1931; Mossop 1921, 1922; Orton 1923, 1926; Gutsell 1931; Weymouth et al. 1931; Weymouth and Thompson 1931; Moore 1934, 1958; Newcombe 1935, 1936; Davenport 1938; Tang 1941; Matteson 1948; Shuster 1951; Fairbridge 1953; Savilov 1953; Haskin 1954; Mason 1957; Lubinsky 1958; Sastry 1961; Craig and Hallam 1963; Merrill et al. 1965; Clark 1968, 1969a,b, 1974, 1975; Olsen 1968; Andrews 1972; Seed 1973, 1976; Thiesen 1973; see Weymouth (1923) for earlier compendium; see also Chapter 5 of this Manual for discussions of external growth patterns]. Excellent discussions on the interpretation of such growth patterns, as well as the effects of various environmental variables on shell growth and surface morphology, are presented by Hedgepeth (1957), Moore (1958), Hallam (1965), and Clark (1974). Despite these extensive studies, the usefulness of external shell growth patterns in ecological and paleoecological studies has been limited.[1] The principal difficulty encountered in interpreting shell surface growth features arises from an inability to distinguish spawning and disturbance lines from annual patterns (Lutz 1976a). Problems associated with distinguishing these growth features have been reduced over the past two decades by the discovery of periodic patterns of growth within the shells, i.e. internal growth patterns, of numerous Recent and fossil molluscs (Barker 1964, 1970; Berry and Barker 1968, 1975; House and Farrow 1968; Pannella and MacClintock 1968; Rhoads and Pannella 1970; Farrow 1971, 1972; Evans 1972; Cunliffe 1974; Pannella 1975; Lutz 1976a; Lutz and Rhoads 1977; Gordon and Carriker 1978; Jones et al 1978). In addition to facilitating interpretation of the temporal significance and causes for observed surface morphological features, such internal growth patterns have proven useful in: (1) geophysical studies for defining Phanerozoic changes in the rate of the earth's rotation (Berry and Barker 1968, 1975; Pannella and MacClintock 1968; Pannella et al. 1968; Pannella 1972, 1975; Dolman 1975; Rosenberg and Runcorn 1975; Weinstein and Keeney 1975; Whyte 1977); (2) ecological and paleoecological studies for assessing the effects of various biological and environmental stresses (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Farrow 1972; Kennish and Olsson 1975; Kennish 1977a, b,c, 1978; see also Chapter 3); and (3) archeological studies for reconstructing settlement patterns of prehistoric hunter-gatherers (Coutts 1970, 1975; Coutts and Higham 1971; Koike 1973, 1975; Ham and Irvine 1975; Clark 1977, 1979).

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[1] Limitations discussed do not apply to external growth patterns of all species. Many bivalves (e.g. certain pectinids) have periodic external shell patterns which are potentially extremely useful in both ecological and paleoecological studies.

Although internal shell growth patterns may potentially be found within all classes of molluscs, the Bivalvia have been by far the most universally studied. This apparent research bias is largely a reflection of the relative ease with which a complete record of bivalve growth can be obtained. Such an ontogenetic record is revealed by sectioning or fracturing the shell along a plane passing from the oldest part of the shell, the umbo, to the growing margin along the axis of maximum growth (Pannella and MacClintock 1968; Rhoads and Pannella 1970; see Chapter 1 for illustration of maximum axis of growth and the Appendices for details of preparation procedures). Complete ontogenetic records are difficult, if not impossible, to obtain from tightly coiled or otherwise torqued shells (e.g. gastropods) using current methods.

The primary purpose of the present chapter is to provide a comprehensive review of the types of internal growth patterns thus far described within molluscan (primarily bivalve) shells. We will also speculate on the origins of these growth patterns. Realized, as well as potential, ecological and paleoecological applications are discussed at some length.[2] In the following discussion, internal growth patterns have been assigned to one of two categories: (1) microgrowth increments and their sequential changes; or (2) shell structural changes. Growth patterns within the former category are associated with alternating regions containing variable concentrations of organic material, while those patterns within the latter category are associated with changes in shell microstructure (e.g. nacreous, prismatic, crossed lamellar, etc.) within a given shell layer or shifts in the relative position of shell layer boundaries on the depositional surface.[3] When viewed in acetate peel or thin section preparations (see Appendices 1 and 2), microgrowth increment patterns often appear superimposed on shell structural changes.

It should gradually become evident to the reader of this chapter that most, if not all, growth patterns within the molluscan shell are a reflection of complex interactions between environmental variables and the organism's physiology. A change in the external environment will often induce physiological (particularly respiratory) changes which result in altered concentrations of metabolic end-products within the extra-pallial fluid. Such fluid chemistry changes can, in turn, have profound effects on the composition and structure of the shell. In the following discussion, we will consider in detail the types of internal growth patterns, resulting from such shell compositional and structural changes, which various workers have described.

II. MICROGROWTH INCREMENTS

Microgrowth increments within the molluscan shell were first described in detail by Barker (1964) in his thin section observations of four genera of bivalves (Mactra, Mercenaria, Anadara, and Chione). Since Barker's original study, similar "microscopic periodicity structures" have been found in numerous other molluscs, and the micro- and ultrastructures of such increments have been described in detail [see Clark (1974) for review]. It is now generally accepted that many, if not all, microgrowth increments within the molluscan shell are a reflection of variations in the relative proportions of organic material (conchiolin) and calcium carbonate (aragonite or calcite). Alternation of calcium carbonate-rich regions and organic-rich regions or lines has been well documented for numerous Recent and fossil species through optical and electron microscopy studies of thin sections, acetate peels, and polished and etched surfaces of the shell (see Appendices 1 to 3 for preparation techniques). These growth lineations were originally interpreted as reflections of solar time (House and Farrow 1968; Pannella and MacClintock 1968; Pannella et al. 1968; Farrow 1971). More recent studies, however, have revealed a complex relationship between incremental shell growth and lunar and solar cycles (Clark 1974, 1975; Pannella 1975, 1976; Thompson 1975; Whyte 1975). Although a one-to-one correspondence has not been established, the formation of microgrowth increments in bivalves is highly correlated with shell valve movements (Thompson 1975; Gordon and Carriker 1978).[4] Because the valves of many species are usually closed during low tide and open during high tide, a high positive correlation also exists between the number of increments and the number of tides to which an organism has been subjected (Evans 1972, 1975; Fig. 2). While valve-movement rhythmicity is usually most pronounced in intertidal individuals, subtidal specimens of at least one species [Mercenaria mercenaria (L.)] exhibit biological rhythms in relative synchrony with the tidal cycle (Thompson 1975).[5] There has been general agreement among growth-line workers that when the valves are open and the organism is actively pumping, shell material is deposited that is rich in calcium carbonate relative to the adjacent shell material (which contains higher concentrations of organic material). Until recently, however, hypotheses attempting to explain the origin of layers relatively rich in organic content have been based on the assumption that calcium carbonate and organic material were deposited at variable rates within daily or tidal cycles (Pannella and MacClintock 1968; Evans 1972; Pannella 1975, 1976), although a few references were made to the possibility that shell dissolution might play a role in the formation of organic-rich layers (Rhoads and Pannella 1970; Wilbur 1972; Rhoads 1974; Thompson 1975). In 1977, Lutz and Rhoads published

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[2] For an in-depth discussion of the manner in which many of these internal patterns can be utilized in studies of population dynamics, see Chapter 3.

[3] While microgrowth increments may be considered "structural" features, we have avoided the use of the term "structure" when referring to such increments in order to avoid confusion. In this chapter we use the term structure in reference to shell structural types (i.e. shell microstructures) or in reference to the arrangement of shell layers.

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[4] Difficulty in establishing a one-to-one correspondence between the formation of increments and valve movements arises as a result of the lack of clearly defined microgrowth increments, when viewed in shell section, near the shell margin. The absence of growth lines in this region has been reported by several workers (Thompson 1975; Gordon and Carriker 1978) and may be related to the lack of polymerization of the organic matrix of the shell near the growing margin (Gordon and Carriker 1978).

[5] Gordon and Carriker (1978), in their laboratory study of Mercenaria mercenaria, did not find the circadian locomotor (valve-movement) rhythms reported by Thompson (1975).

While structures such as interlamellar, intercrystalline, and interprismatic organic matrices are universally recognized, the structural organization of intracrystalline and intraprismatic organic material has been the subject of some controversy (Watabe 1963, 1965; Towe and Hamilton 1968a, b; Travis 1968; Travis and Gonsalves 1969; Mutvei 1970; Towe 1972; Towe and Thompson 1972). Sometimes this organic material assumes the form of coherent matrices or "envelopes" located within prisms or aragonitic nacreous tablets. However, some workers (Towe and Hamilton 1968a, b; Towe 1972; Towe and Thompson 1972) have suggested that such organic matter, when present, may represent impurities in the carbonate in the form of trapped proteins or polypeptides. It was originally suggested that such intracrystalline organic matter was water-soluble (Crenshaw 1972), but subsequent studies have refuted this hypothesis and indicate that the water-soluble fraction appears to be adsorbed on crystal surfaces (Erben 1974; M.A. Crenshaw, personal communication).

Lutz-Rhoads Hypothesis--

With the above discussion serving as a background, we offer the following as an explanation of growth line formation in the molluscan shell. During aerobic metabolism, molluscs deposit calcium carbonate in the form of aragonite or calcite, together with organic material, resulting in shell construction. Aerobic metabolism is usually associated with periods of active pumping during high tide in well-oxygenated waters. As the concentration of dissolved oxygen falls, such as in the internal micro-environment created by the organism during periods of shell closure, anaerobic respiratory pathways are employed and the level of succinic acid (or other acidic end-products) within the extrapallial fluid rises. The acid produced is gradually neutralized by the dissolution of shell calcium carbonate, leading to increased levels of Ca^{2+} and succinate (or other end-products) within the extrapallial and mantle fluids (Fig. 4; see also Crenshaw and Neff 1969). As a result of this decalcification, the ratio of relatively acid-insoluble organic material to calcium carbonate increases at the interface between the mantle and shell.[6] One need not invoke the complication of an increased concentration of organic material in a given volume, although a collapse of unsupported matrix structures or a movement of the mantle as a compensatory response to the increased distance between mantle and shell could result in increased concentrations of freed organic material in specific regions of the extrapallial fluid. With the opening of the valves and the resumption of aerobic metabolism (see Fig. 3), the deposition of calcium carbonate and organic material within an area containing an insoluble residue of organic material should result in a localized increase in the ratio of organic material to calcium carbonate within the specific shell region. The end-product of this process, a hypothesis of growth-line formation which proposed that organic concentrations in various regions of the shell were simply residues left behind as a result of dissolution of shell material during periods of anaerobiosis. Independent quantitative evidence in partial support of this hypothesis has recently been presented by Gordon and Carriker (1978). In the following section, we summarize the mechanism of growth line formation as outlined by Lutz and Rhoads (1977).

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[6] It is also conceivable that the ratio of organic material to calcium carbonate at the mantle-shell interface could increase as a result of cessation of calcium carbonate deposition, with continued deposition of organic material. This hypothesis does not require shell dissolution and might be invoked to explain growth line formation, as well as to explain some of the ultrastructural observations described elsewhere in this chapter. Evidence in support of this hypothesis, however, is unavailable at present.

Formation of Microgrowth Increments

Prior to describing the physiologically-controlled mechanism of growth line formation, it is necessary to provide a brief background based on recent studies of molluscan anaerobiosis and shell organic-inorganic relationships. In the following paragraphs, we consider the implications of these studies in detail.

Anaerobic Respiration in Molluscs--

The ability of molluscs to respire anaerobically has been well documented. Excellent reviews of this subject have been presented by von Brand (1944), Hochachka and Mustafa (1972), and de Zwann and Wijsman (1976). The biochemical pathways operating during anaerobiosis, at least in bivalves, appear different from those described in vertebrates. In contrast to vertebrate pathways, in which quantities of lactic acid are produced during anaerobic metabolism, the major end-products of molluscan anaerobic respiration are succinic acid and alanine (Stokes and Awapara 1968; de Zwann and Zandee 1972; de Zwann and van Marrewijk 1973). Early studies (Collip 1920, 1921) suggested that calcium carbonate from the shell served to buffer the acidic products of anaerobic metabolism, and visible corrosion of the growth surfaces of Mercenaria mercenaria was observed after prolonged periods of shell closure (Dugal 1939). This hypothesis has been confirmed through studies of chemical changes in the composition of the extrapallial fluid (Crenshaw and Neff 1969; Gordon and Carriker 1978; see also Figs. 3 and 4) and measurement of Ca^{45} deposition and solution (Crenshaw and Neff 1969); at least a portion of the succinic acid produced during anaerobic metabolism is neutralized by dissolution of $CaCO_3$ from the shell. Furthermore, measurements of the oxygen tension and succinate levels in the extrapallial fluid have demonstrated that M. mercenaria becomes anaerobic when the valves are closed (Figs. 3, 4). As alluded to by Wilbur (1972), periodic valve closure should, therefore, result in an alternation of shell deposition and decalcification. Any theory on growth line formation must account for decalcification at the interface between the mantle and shell and its effect on preservation of the complete record of growth found within the shells of numerous species (Berry and Barker 1968; Pannella and MacClintock 1968; Rhoads and Pannella 1970; Farrow 1971, 1972; Kennish and Olsson 1975; Kennish 1978).

Organic-Inorganic Relationships--

Recent shell structure research has contributed greatly to our understanding of micro- and ultrastructural relationships between organic material and inorganic crystals of calcium carbonate within the shells of bivalves, gastropods, and cephalopods (Watabe and Wilbur 1960, 1961; Oberling 1964; Hudson 1967, 1968; Wise and Hay 1968a, b; Kennedy et al. 1969; Mutvei 1969, 1970, 1972; Taylor et al. 1969; Gregoire 1972; Crenshaw and Ristedt 1975).

from a strictly structural viewpoint, is one growth increment.[7]

Supporting Evidence--

As mentioned earlier, evidence in partial support of the above hypothesis has recently been provided by Gordon and Carriker (1978) based on measurements of extrapallial fluid pH,[8] rates of shell dissolution during valve closure [from the data of Crenshaw and Neff (1969)], the thickness of subdaily growth lines, and duration of valve closure of *Mercenaria mercenaria*. In their study, Gordon and Carriker measured thicknesses of organic-rich "subdaily growth striations" ranging from 0.45 to 0.9 µm. Crenshaw and Neff (1969) calculated that, at measured rates of calcium dissolution, an organism with a shell weight of 100 g would lose about 2 mg of shell per hour. Shell weights of *M. mercenaria* specimens used by Gordon and Carriker (1978) ranged from 40 to 80 g, with internal shell surface areas of 44 to 64 cm^2. Assuming the dissolution rate to be uniform over the entire internal surface, Gordon and Carriker calculated the thickness of shell that would be removed for every hour the shell is closed:

$$\frac{\text{Shell loss per hour}}{\text{unit weight}} \times \frac{\text{total weight}}{\text{surface area}} \times \frac{1}{\text{density}} = \text{thickness lost per hr.}$$

For example, one specimen with valves weighing 64 g and an internal surface area of 56 cm^2 would lose 7.8×10^{-2} µm/hr (using a density of 2.93 g/cm^3 for aragonite). Experimental organisms in their (Gordon and Carriker, 1978) study kept their valves closed for 2.5 to 12 hr. At the calculated rate of shell dissolution, the thickness of shell removed would be 0.2 to 0.94 µm. These values are sufficiently close to the measured widths (0.45 to 0.9 µm) of subdaily lines to suggest a causative relationship between the dissolution and subdaily line thickness.

As a result of the above measurements and calculations, Gordon and Carriker (1978) conclude that:

> "To account for subdaily striations, then, it is only necessary to envision continuous and simultaneous secretion of organic matrix and calcium carbonate during the aerobic shell-building part of the animal's growth cycle. In the anaerobic period, increasing acid in the extrapallial fluid dissolves a portion of newly deposited shell. Some of the associated matrix may also dissolve, but at least part of it is sufficiently insoluble to resist attack by metabolic acids and remains behind as a residue, to be covered by a new

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[7] The presence of intraprismatic and intracrystalline coherent organic matrices would generally be more compatible with this hypothesis than would reincorporation into the shell of organic inclusions freed during decalcification, although the latter interpretation is certainly tenable.

[8] As calibration buffers of suitable ionic strength were not used in their study, Gordon and Carriker (1978) actually measured electrode potential rather than hydrogen ion concentration.

> layer of calcified material during the next cycle of aerobic deposition. Because the matrix at this point is hardened by polymerization of the protein, it maintains its structural integrity during and after decalcification. As a result, the width of residual matrix provides a record of the length of time that the shell was exposed to metabolic acids."

Thus, results and conclusions from Gordon and Carriker's (1978) study lend considerable support to the hypothesis of growth line formation outlined above.

Further evidence suggesting the importance of respiratory changes in producing microgrowth increments is provided by a reinterpretation of the works of Bevelander and Nakahara (1969; Nakahara and Bevelander 1971). In their electron microscope study of the formation and growth of the prismatic layer of Pinctada radiata (Leach) Nakahara and Bevelander (1971) envisioned fragments of "electron-dense lamellae" at the internal boundary of future prisms (Figs. 5, 6) as migrating through the extrapallial fluid and ultimately forming envelopes within which crystal nucleation and growth occur. If their presented micrographs (Figs. 5, 6) are reinterpreted and the described process of prism formation is envisioned as occurring in reverse, we can observe quite vividly the process of gradual shell destruction. As calcium carbonate slowly dissolves, relatively insoluble organic envelopes, matrices, or inclusions remain at the mantle-shell interface, presenting the appearance of an electron-dense lamella (Figs. 5, 6). That this organic residue is subsequently incorporated into the shell, as proposed by our hypothesis, is strongly suggested by the presence of "intraprismatic organic strands" approximately paralleling the inner growth surface of the prisms (Fig. 6c). While details of the treatment of the studied pearl oysters prior to anesthetization were not presented by Nakahara and Bevelander (1971), one can reasonably assume that laboratory conditions and/or exposure to air prior to or during the placement of the organisms in magnesium sulfate could have induced valve closure and subsequent anaerobiosis.

Results of an earlier study conducted by Bevelander and Nakahara (1969) on the formation and growth of nacre have been interpreted as illustrative of shell dissolution (Erben 1972, 1974; J.D. Taylor, personal communication). That their organic "compartments" (Fig. 7) at the mantle-shell interface may indeed be reflections of shell dissolution is suggested by an examination of the treatment of their studied bivalves prior to fixation. For a period of 1 hour before fixation, the molluscs were placed in a refrigerator at 5°C. As implied earlier (see also Crenshaw and Neff 1969), such treatment is almost certainly sufficient to induce anaerobiosis, with release of succinic acid into the extrapallial fluid. Neutralization of this acid by calcium carbonate from the shell would be expected to result in selective shell destruction in a manner virtually identical to that seen in Figure 7. While microgrowth increments have seldom, if ever, been reported in nacre, they do occur.

Nonreflected growth lines[9] within the middle nacreous layer[10] of the Atlantic ribbed mussel, Geukensia (= Modiolus) demissa (Dillwyn) (Fig. 8) show clustering patterns similar to those reported in a number of species (Pannella and MacClintock 1968; Evans 1972, 1975; Clark 1974; Pannella 1975, 1976). Mechanisms of growth line formation within nacreous structures may or may not be precisely analogous to the process within the prismatic layer of Pinctada. If intracrystalline organic matrices are present, the process may be almost identical to that occurring in Pinctada prisms. In light of the current controversy over the presence or absence of such organic structures [see Towe (1972) for discussion], we suggest an alternative mechanism of growth line formation in nacre.

It has been proposed that nacreous crystal nucleation occurs on the surface of an organic substratum and that during growth these crystals are enclosed within tight-fitting organic envelopes (Erben 1972, 1974; Mutvei 1972; Erben and Watabe 1974). As a result of the lateral fusion of the crystals to form a mature nacreous lamina, adjacent lateral and distal portions of the envelopes merge to become intercrystalline and interlamellar organic matrices, respectively. If crystal nucleation and growth occasionally occur within organic compartments remaining after decalcification, and subsequent growth proceeds as described above, lateral fusion of adjacent crystals should result in a marked increase in the thickness of interlamellar and intercrystalline organic matrices. Such an increased concentration of conchiolin relative to calcium carbonate could explain growth patterns observed on acetate peels of polished and etched sections of G. demissa nacre. Evaluation of the above alternation of shell dissolution and deposition in the perspective of the current controversy associated with the template and compartment hypotheses (Bevelander and Nakahara 1969; Nakahara and Bevelander 1971; Mutvei 1972; Towe 1972; Erben and Watabe 1974) suggests that, while compartments may exist from a strictly structural viewpoint, they are not primary features, but rather "residual" in nature, and should be considered of only incidental importance in the formation of nacre. A similar point of view concerning the presence (or lack) of preformed matrix layers or compartments has been expressed by Gordon and Carriker (1978).

Summary of Documented Microgrowth Increment Patterns

The following discussion is intended to provide a current literature review[11] of microgrowth increment patterns described to date within the molluscan shell. Detailed descriptions and micrographs of the various types of patterns may be found in Chapter 3. For the purposes of this review, we have assigned documented microgrowth increment patterns to one of the following five temporal categories: (1) semidiurnal and diurnal; (2) fortnightly; (3) monthly; (4) annual; (5) semiperiodic or random events.[12]

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[9] See Pannella and MacClintock (1968) for a detailed description of nonreflected growth lines within the bivalve shell.

[10] L. F. Gainey, Jr. and M. J. Greenberg (personal communication) have indicated that this middle layer is equivalent to the "inner nacreous layer" described by Blackwell et al. (1977). See also Lutz and Rhoads (1978) for a critique of the study by Blackwell et al. (1977), as well as a detailed description of the shell structure of Geukensia demissa (Dillwyn).

[11] For earlier compendia, see Rhoads and Pannella (1970) and Clark (1974).

Semidiurnal and Diurnal--

As mentioned above, Barker (1964) has been credited with the discovery of microgrowth increments (and their sequential patterns) within the molluscan shell. As a result of his examination of several species of bivalves, Barker (1964) suggested that these small scale internal growth features might reflect semidiurnal and/or diurnal periodicities. Since 1964, considerable research has been conducted to test the validity of this hypothesis.

The first convincing evidence that diurnal periodicities were indeed recorded within the molluscan shell was provided by Pannella and MacClintock (1968). In their study of _Mercenaria mercenaria_, these workers counted from 360 to 370 lines and from 720 to 725 lines for growth periods of 368 and 723 days, respectively. These results strongly suggested that such microscopic growth increments were formed with a solar periodicity. "Solar" daily increments were also described by Pannella and MacClintock (1968) in _Tridacna squamosa_. More recently, other workers have examined and analyzed growth patterns in _M. mercenaria_ and _T. squamosa_ in greater detail, increasing our understanding of factors responsible for the formation of diurnal (and semidiurnal) increments in these and other species of molluscs (MacClintock and Pannella 1969; Rhoads and Pannella 1970; Thompson and Barnwell 1970; Evans 1972, 1975; Pannella 1972, 1975,[13] 1976; Cunliffe and Kennish 1974; Kennish and Olsson 1975; Thompson 1975; Kennish 1976, 1977b, 1978; Gordon and Carriker 1978). It is now generally accepted that such microgrowth increments are largely reflections of complex interactions between lunar and solar cycles (Clark 1974, 1975; Pannella 1975, 1976; Thompson 1975; Whyte 1975). At about the same time that Pannella and MacClintock (1968) reported the results of their study of growth patterns in _M. mercenaria_, House and Farrow (1968) independently suggested that similar microscopic features within the shell of _Cerastoderma_ (= _Cardium_) _edule_ were formed daily. Since these early studies, periodic microgrowth increments have been found in many other Recent and fossil species of molluscs. Pannella et al. (1968) reported the presence of well-preserved "daily" growth increments in 12 species of molluscs from several geological periods (Middle Devonian to Upper Miocene). Barker (1970) prepared thin sections of the shells of over 98 species of bivalves and described numerous subannual structures within these shells which he felt might be related to daily or tidal cycles within the environment. Other detailed studies providing evidence for the presence of diurnal and/or semidiurnal periodicity structures within molluscan shells include those of Rhoads and Pannella (1970), Farrow (1971, 1972), Evans (1972, 1975; see also Fig. 2), Pannella (1975), Whyte (1975), and Lutz and Rhoads (1977).

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[12] A few workers (Pannella and MacClintock 1968; Kennish and Olsson 1975; see also Chapter 3) offer a description of bidaily patterns in _Mercenaria mercenaria_. Such patterns have not been described in detail in other species and will not be discussed in this section. Similarly, growth patterns reflecting a semiannual cycle [see Clark (1974) for a discussion of this type of periodicity] have not been well-documented and are not considered in the present discussion.

[13] Pannella (1975) also describes daily increments within the shell of the closely related venerid, _Mercenaria campechiensis_.

Fortnightly--
Microgrowth patterns recurring at approximately fortnightly intervals have been described in a large number of molluscs, particularly those inhabiting intertidal and shallow subtidal environments (Barker 1964; Berry and Barker 1968; Pannella and MacClintock 1968; Pannella et al. 1968; House and Farrow 1968; Rhoads and Pannella 1970; Evans 1972, 1975; Clark 1974; Kennish and Olsson 1975; Kennish 1976, 1977b; Pannella 1975, 1976; see also Chapter 3). Barker (1964), in his detailed examination of "microtextural variation" in the bivalve shell, described "3rd-order layers" composed of microgrowth increments cyclically varying in thickness and hypothesized that such "layers" might recur at intervals of approximately 15 days. More recently, Pannella and MacClintock (1968), and later Pannella (1975), published detailed micrographs of acetate peels of sectioned *Mercenaria mercenaria* and *Tridacna squamosa* showing fortnightly "clusters" of microgrowth increments within the outer shell layers of these two Recent bivalves.[14] These workers described similar "fortnightly cycles of deposition" within the shells of numerous fossil specimens[15] and presented micrographs of "fortnightly" patterns within *Mercenaria campechiensis ochlockoneenis* (Upper Miocene), *Crassatella mississippinesis* (Upper Eocene), *Limopsis striatopunctatus* (Upper Cretaceous) and *Conocardium* sp. (Upper Pennsylvanian). Similar clustering (fortnightly?) patterns of microgrowth increments have been observed within the middle nacreous layer of the Recent mytilid *Geukensia demissa* (Fig. 8; see also Lutz and Rhoads 1977). Evans (1972, 1975) presented a micrograph (Fig. 2 in this chapter) of an acetate peel of *Clinocardium nuttalli* which illustrates a fortnightly pattern of microgrowth increments within the outer shell layer of this cockle. Pannella (1976) published a similar micrograph of *Limopsis striatopunctatus* (Upper Cretaceous) showing an inferred "fortnightly" pattern of growth. Dolman (1975), in his Fourier analysis of microgrowth periodicities in *Cerastoderma* (= *Cardium*) *edule*, recognized weakly-developed fortnightly growth cycles in this species. Pannella (1975) photographically illustrated fine structures[16] within the shell of an unidentified Middle Devonian cephalopod and suggested that observed clusters of these structures might reflect a fortnightly periodicity. Earlier

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[14] Kennish and Olsson (1975) and Kennish (1976, 1977b) provide additional discussions of fortnightly patterns of microgrowth increments in *Mercenaria mercenaria* (see also Chapter 3).

[15] The "fortnightly" periodicity of patterns in these fossil specimens was inferred from their structural similarity to those patterns that Pannella and MacClintock (1968) observed within the shells of *Mercenaria mercenaria*.

[16] Such fine structures were shell surface topographic features and need not correspond with microgrowth increments within the shell.

brief reviews of fortnightly patterns within the molluscan shell are presented by Rhoads and Pannella (1970) and Clark (1974).

Monthly--

Numerous workers have provided evidence for the presence of monthly microgrowth patterns within the shells of various species of molluscs (House and Farrow 1968; Pannella and MacClintock 1968; Pannella et al. 1968; Rhoads and Pannella 1970; Farrow 1972; Kennish and Olsson 1975; Kennish 1976, 1977b; see also Chapter 3). House and Farrow (1968), in their analysis of microgrowth increments within the shell of Cerastoderma edule, observed "a regular bunching" of growth increments which occurred with a frequency of 29 days. Farrow (1972), in a later study of this same bivalve, showed that this monthly periodicity could be related to prolonged exposure due to very low high tides at every other neap tide for part of the year. Pannella and MacClintock (1968) reported a similar (synodic) monthly periodicity in Mercenaria mercenaria characterized by groupings of fortnightly "clusters" in pairs, with one fortnightly cluster more pronounced than the other. This internal pattern is also expressed, at least on some parts of the outer surface of this species, by concentric undulations with a wavelength periodicity of 29 days (see also Kennish and Olsson 1975; Kennish 1976, 1977b; Chapter 3). Pannella et al. (1968) reported the presence of "synodic-month patterns" in numerous fossil molluscs ranging in geologic age from the Middle Devonian to Upper Miocene. The "monthly" periodicity of patterns within the shells of these fossil specimens was inferred from the structural similarity of patterns to those patterns that Pannella and MacClintock (1968) observed within the shells of Mercenaria mercenaria. Rhoads and Pannella (1970) photographically illustrated "monthly clustering" patterns of microgrowth increments formed during the autumn months in Nucula proxima from 6 meters of water in Long Island Sound. More recently, Kahn and Pompea (1978) have suggested that septal formation within the cephalopod Nautilus pompilius may take place at monthly intervals[17] and reported the presence of similar "monthly" structures within the shells of numerous fossil cephalopods (Upper Ordovician to Upper Miocene). Possible factors responsible for the formation of monthly growth patterns in molluscs are discussed by Pannella and MacClintock (1968), Clark (1974), and Pannella (1976).

Annual--

Annual patterns of microgrowth increments have been observed within the shells of the majority[18] of specimens which have been examined and analyzed in detail. Such patterns are generally a result of seasonal variations in growth which, in turn, usually result in the formation of relatively thick microgrowth increments during certain seasons (e.g. northern hemisphere, high latitude, summer) and relatively thin increments during others (e.g. northern hemisphere, high latitude, winter). These annual patterns constitute the "1st-order layers" described by Barker (1964) in his detailed examination of Mercenaria mercenaria, Mactra solidissima, Chione cancellata, and Anadara ovalis. Pannella and MacClintock (1968), and later Rhoads and Pannella (1970), Kennish and Olsson (1975), and Kennish (1976, 1977b; see also Chapter 3), presented detailed micrographs illustrating these patterns within M. mercenaria. Similar annual patterns were described in detail by House and Farrow (1968) and Farrow (1971, 1972) in their examination of microgrowth increments in Cerastoderma edule. Spawning patterns, while sometimes occurring with an annual periodicity in certain species of bivalves, are considered in this chapter to be more accurately described as semiperiodic events and will therefore be considered in the next section. Further discussions of annual growth patterns within the molluscan shell may be found in Rhoads and Pannella (1970), Clark (1974), and in Chapter 3.

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[17] Similarly, Martin et al. (1977), in their study of Nautilus macromphalus, interpreted observed periodic weight fluctuations, occurring at intervals of approximately 30 days, to indicate the formation of new septa.

[18] Annual patterns have generally not been recognized in deep-water molluscan species; in such species, major growth patterns have been interpreted to mark spawning events (Rhoads and Pannella, 1970).

Semiperiodic or random events--

Many patterns are encountered within the shells of molluscs which do not occur with definite cyclic periodicities. "Sub-daily" growth increments described by numerous workers may be examples of such aperiodic features (Pannella and MacClintock 1968; Kennish and Olsson 1975; Kennish 1976, 1977b; Gordon and Carriker 1978; see also Chapter 3). Distinct microgrowth patterns also result from damage to the shell margin (see Chapter 3 for detailed illustrations and discussions of these patterns). Notching of the shell with a small file, for instance, causes formation of a distinct disturbance line and microgrowth pattern (see Pannella and MacClintock 1968; Kennish and Olsson 1975; Kennish 1976, 1977b, see also Chapter 3). Shell damage caused by predator attacks may result in similar growth patterns. Storm events are often recorded in the shell and can sometimes be recognized by the presence of associated silt particles which are trapped between the mantle and the shell during the storm and then are subsequently incorporated into the shell (Barker 1964; House and Farrow 1968; Rhoads and Pannella 1970; Kennish and Olsson 1975; see also Chapter 3). Certain pollution events, such as the discharge of heated effluent waters from nuclear or fossil fuel power plants, may also result in the formation of microgrowth patterns within the shell (Kennish and Olsson 1975; see also Chapter 3). Rhoads and Pannella (1970) demonstrated that the transplantation of organisms to different environments will often result in marked differences in the pattern of microgrowth increments before and after transplantation. Spawning events, which may be considered semiperiodic, have been found to be reflected in microgrowth patterns within almost all molluscan shells which have been examined in detail. Even bivalves (e.g. Malletia sp.) from depths as great as 4970 meters have patterns which have been interpreted to mark spawning events (Fig. 9; see also Rhoads and Pannella 1970). Pannella and MacClintock (1968), and later Rhoads and Pannella (1970), Kennish and Olsson (1975), and Kennish (1976, 1977b, 1978; see also Chapter 3) presented detailed descriptions and illustrations of the appearance of spawning patterns in a few species of shallow-water bivalves. For a further detailed discussion of the types of semiperiodic and random events which can be recorded within the molluscan shell, see Chapter 3.

Ecological and Paleoecological Applications

Ecology has been defined as the study of relationships between organisms and their environment. In functioning ecosystems, it is possible to make direct observations of these relationships and their temporal changes. Organism-environment relationships may not always be directly measured, however, requiring an indirect or deductive approach; for instance, one may wish to assess the effect of a storm, pollution event, change in salinity, temperature, etc. on a population after the event has taken place. In the absence of data about pre-disturbance rates of growth, death, and reproduction, one is totally dependent on indirect techniques. This kind of after-the-fact problem is common in paleoecology and promises to be an increasingly important approach in ecological studies. In this section, we will consider the various ways in which detailed analyses of molluscan microgrowth patterns have been applied to ecologic and paleoecologic studies, and we will speculate on their future applications.

Microgrowth increments have proven especially useful in recognizing how seasonally variable environmental factors affect molluscan growth. For instance, through analysis of patterns of "daily" microgrowth increments, Farrow (1971) found that a substantial portion of a population of the shallow subtidal cockle, Cerastoderma edule, from the Thames estuary in England stopped growing during winter because of sub-zero temperatures. Similarly, Tevesz (1972) observed that Gemma gemma (Totten) grew very little in the winter; growth increments were very closely spaced and the inner shell layer had a brownish hue. During the summer, G. gemma grew rapidly; microgrowth increments were widely spaced, and the inner shell layer was clear and translucent in appearance. Through an examination of microgrowth increments in numerous acetate peels, Evans and LeMessurier (1972) were able to demonstrate striking winter growth rate differences between two sympatric species of bivalves. They found winter growth of the rock-boring clam, Penitella penita, to be approximately 75% of the summer growth rate, while the growth rate of the cockle, Clinocardium nuttalli, which inhabited a neighboring mud flat, decreased during the winter, relative to the summer, by as much as a factor of 19. For further examples and discussions of the usefulness of microgrowth increments for reconstructing seasonal variations in molluscan growth, see House and Farrow (1968), Pannella and MacClintock (1968), and Rhoads and Pannella (1970).

Microgrowth increment patterns can also supply detailed information on the age of individuals at the time of death, as well as the season of their death. In those species for which the periodicities of microgrowth patterns have been established, the age at death is readily obtained by simply counting the total number of patterns. The periodicity with which the counted patterns occur (daily, fortnightly, annual, etc.) will determine the precision of the age estimate. The season of death is determined by relating the position of the last increment at the margin of the shell to the seasonal growth pattern (Fig. 10). For example, a margin preceded by a complete summer depositional record represents death early in the fall. A margin which follows a long period of winter growth represents late winter or early spring death. Often, however, when the shell margin is preceded by a few days of growth slowdown, comparison of several individuals may be necessary in order to determine if growth rate changes reflect a moribund condition prior to death or are related to seasonal changes (Rhoads and Pannella 1970). By counting the number of microgrowth increments (or patterns of increments), it is also often possible to relate the season of death to absolute age at death. Furthermore, the identification of the season of death and age at time of death in a mollusc assemblage may be used to distinguish a mass mortality from a death assemblage produced by natural mortality. As emphasized by Rhoads and Pannella (1970). this information may be used to determine seasons of peak environmental stress. This technique can be especially useful when applied to drilled shells. By determining the season of death of drilled members of a population, one may identify the season of peak predator activity (Rhoads and Pannella 1970).

Microgrowth increment patterns can also frequently be utilized to determine the age at sexual maturity and season of reproduction by relating the position of spawning breaks to absolute age and the seasonal pattern of growth. An illustration of how growth patterns have been used for such purposes is provided by Rhoads and Pannella (1970) in their analysis of microgrowth patterns in the shell of *Gemma gemma*.

Variations in environmental parameters including food supply, substratum type, salinity, dissolved oxygen, turbidity, temperature, and population density can influence the growth of bivalves. Hallam (1965) reviews these various environmental parameters as causes of stunting and dwarfing of living and fossil marine benthic invertebrates. Several studies conducted over the past few years have used microgrowth increments to define the effects of various environmental perturbations, such as those outlined by Hallam (1965), on bivalve growth. Rhoads and Pannella (1970), for example, through careful examination of microgrowth patterns on both acetate peels and thin sections, have shown that *Mercenaria mercenaria* grows faster in sandy sediments than in mud when other variables are eliminated. Also, these workers analyzed microgrowth increment patterns within *Astarte castanea* (Say) and *M. mercenaria* to demonstrate that growth rate (and shell structural) changes occur when specimens of these species are transplanted from a natural subtidal environment to a laboratory holding tank without substratum (Fig. 11). Farrow (1971) used microgrowth increments within the shell of *Cerastoderma edule* to illustrate that high density populations of this species had a much shorter growing season than low density populations. An inverse relationship between individual cockle size and cockle population density was also noted. In a subsequent study, Farrow (1972) used microgrowth increments within the outer shell layer of *C. edule* to demonstrate that individuals living in the high intertidal zone were stunted relative to low intertidal individuals. The higher shore cockles were situated near the high water mark and, consequently, were aerially exposed for several days during neap tides. Following neap tide deceleration, there was a resumption of vigorous growth. Many of the high intertidal cockles were some two-thirds the size of individuals in the lower intertidal zone, where growth was more continuous.

Microgrowth patterns can also provide evidence about the biology of deep-water molluscs. Preliminary data of Rhoads and Pannella (1970) indicate that such patterns can shed light on problems related to deep-water periodicity in growth and reproduction, as well as yield information on temporal variations in the deep-water environment. Furthermore, study of the relationship of microgrowth patterns to bathymetry has yielded information on the effect of water depth on calcification (Rhoads and Pannella 1970). Preliminary results suggest that microgrowth patterns within the shells of fossil molluscs may be of use in paleobathymetric studies for defining relative depth gradients in Phanerozoic marine environments. As discussed by Rhoads and Pannella (1970), a bathymetric change from shallow to deep water is accompanied by decreased surface wave motion at the bottom, decreased light penetration, and decreased variation in temperature, salinity and food supply. Depth variation in the fluctuation of the physical-chemical environment should be reflected in features of microgrowth patterns.[19] Microgrowth increments of deep-water species are relatively regular in thickness and have poorly-defined boundaries which are delimited by color variation. Shallow-water bivalves, especially those living in the boreal intertidal zone, show sharply delimited microgrowth increment boundaries and these increments show differences in thickness related to tidal and seasonal periodicities. Data presently available (i.e. Rhoads and Pannella 1970) is limited to species from extremes in bathymetric range. Further work on the relationship of microgrowth patterns to water depth is required for species from intermediate water depths, especially on either side of the seasonal thermocline.

Clark (1974), in his review of growth lines in marine invertebrate skeletons, summarizes a few potential ecologic uses of microgrowth increment patterns which have not been discussed above. For example, he points out that the presence of disturbance lines, or variation in the spacing of periodic lines, can be used as an index of environmental variability; and high variability argues for relatively shallow water. Similarly, the presence of annual patterns of microgrowth increments suggests a climate with well defined seasons, and the presence of increments occurring with a tidal periodicity implies a habitat in or near the intertidal zone. Clark (1974) summarizes his review by stating that "virtually any approach which can be used to demonstrate that growth lines form today as reflections of the environment can be turned about to make interpretations of past environments from fossil lines. . .". Along these same lines, Pannella and MacClintock (1968) have suggested that seasonal and climatic variations of microgrowth patterns can be useful in the study of latitudinal distributions of fossil assemblages. Similarly, Hall (1975) found that the number of microgrowth increments in "biochecks and bands of fast growth" within the shells of *Tivela stultorum* and *Callista chione* varied with age, latitude, and water depth and has suggested that counts of microgrowth increments in similar shell regions of fossil specimens might be of use in reconstructing both paleolatitudes and paleoclimate.

In all of the examples discussed in the preceding paragraphs, observed changes in microgrowth increment patterns result from natural environmental perturbations. With the increased potential environmental impact of many of man's activities (dredge-spoil dumping, oil spills, thermal discharges, disposal of chemical and radioactive wastes, etc.), the number of environmental perturbations of anthropogenic origin has been steadily increasing and these anthropogenic changes in the environment can also be recorded in skeletal growth. One of the best examples of how such pollution events can be manifested within the molluscan shell comes from a recent study conducted by Kennish and Olsson (1975). These workers analyzed in detail microgrowth increments within the shell of Mercenaria mercenaria to define the effects of thermal discharges from a nuclear power plant on the growth of this species. They found that clams from within a mile radius of the mouth of the discharge canal of the nuclear plant had a much higher number of shell growth interruptions, thinner shells, and slower summer growth rates than did clams farther from the plant. By counting growth increments back from the shell margin, they were able to determine that many of the growth breaks[20] were associated with rapidly changing water temperatures which resulted from abrupt shutdowns and startups of the power plant.[21] Kennish and Olsson (1975) also suggested that the thermal effluent may be adversely affecting physiological functions other than growth. At the station nearest the effluent, no spawning breaks were observed within the shells, while such breaks were seen in specimens from all control sites.

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[19] Pannella (1976) has more recently extended and refined these ideas, providing evidence that microgrowth patterns within the shells of fossil molluscs can be used to reconstruct tidal curves of paleoseas.

In summary, the fact that microgrowth increment patterns reflect environmental changes has many applications to ecologic and paleoecologic problems. As we have attempted to emphasize, comparison of growth patterns between specimens collected from different biotopes may be used to identify clinal gradients in growth. Recognition of growth gradients (both spatial and temporal) in Recent and fossil assemblages may greatly assist both the ecologist and paleoecologist in recognizing environmentally related stress gradients. When these and the other applications discussed above are combined, the molluscan shell might well be interpreted as a long term continuous environmental recorder.

III. SHELL STRUCTURAL CHANGES

At this point, it is imperative that the reader recognizes that we are no longer discussing microgrowth increment patterns. A distinction was made, in the introduction to this chapter, between patterns of microgrowth increments and patterns associated with shell structural changes. We thus emphasize once again that shell structural changes, which are considered in the following discussion, as associated either with changes in shell microstructure within a given layer or shifts in the relative position of shell layer boundaries on the depositional surface.[22] As stated earlier, we use the general term

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[20] Such breaks were associated with relatively unique patterns of microgrowth increments within the shell. See Chapter 3, Plate II e-g, for photographic illustrations of this type of break (and associated microgrowth increment patterns) in Mercenaria mercenaria.

[21] The growth rate of M. mercenaria generally increases with increasing temperatures and peaks between 20-24°C.; Haskin (communicated to Kennish and Olsson, 1975) found decreased growth above 26°C. The thermal effluent raised water temperature in areas around the nuclear plant 3-5°C. above ambient.

[22] We include here the addition of a shell layer (e.g. addition of a calcitic layer to cooler water representatives of a largely aragonitic species).

"structure" in reference to shell structural types (i.e. shell microstructures) or in reference to the arrangement of shell layers.

Formation of Structural Changes

For over fifty years, workers have recognized that structural changes observed within the shells of certain bivalves may reflect changes in environmental conditions (Weymouth 1923; Dodd 1964; Davies and Sayre 1970; Kennish and Olsson 1975; Lutz and Rhoads 1977). Only recently, however, have mechanisms responsible for some of these changes been considered in detail. In 1970, Davies and Sayre suggested that various conditions of environmental stress could lead to shell dissolution and, furthermore, that such dissolution events were recorded in the ultrastructure of the shell. More recently, Lutz and Rhoads (1977) have hypothesized that extensive reworking of original shell microstructure occurs as a result of environmentally controlled alternating periods of shell deposition and dissolution associated with utilization of aerobic and anaerobic pathways, respectively. Evidence that such shell destructive mechanisms may be operating in bivalves during periods of environmental stress has been provided by Lutz (1976b, 1977) and Lutz and Rhoads (1977, 1978) through a detailed analysis of seasonal and geographical variation in the shell structure of a Recent mytilid (*Geukensia demissa*). In the following paragraphs we will summarize the results obtained by these workers in order to provide an example of the manner in which environmentally induced metabolic changes might drastically alter the original structure of a bivalve shell. Preparation procedures for analysis of described structural changes may be found in Appendices 1 and 2.

The structure of the inner shell layer of *G. demissa* varies not only with season, but also with latitude. If specimens from relatively cold-water (high latitude) environments such as the Gulf of Maine are examined, the seasonal sequence of events occurring on the growth surface of the inner shell layer is summarized as follows. During the warm summer months (June through September), very regular hexagonal nacreous tablets are arranged in steplike patterns characteristic of bivalve nacre (Fig. 12A). As water temperatures decline, the nacreous tablets become smaller and less regular,[23] showing visible signs of corrosion in the form of marked pitting and hollow crystals (Erben 1972; Wada 1972), as well as increased proportions of fine-grained structures (Fig. 12B-D). An increased stacking of nacreous tablets (i.e. increased proportions of columnar nacre) is also apparent in various areas of the inner layer growth surface (Fig. 13). During the colder months of the year (January to March, with water temperatures below 3°C.), shell corrosion becomes visible to the naked eye, the entire inner shell surface often presenting a chalky white appearance. Ultrastructurally, this surface appears uniformly fine-grained (Fig. 12E). Similar macroscopically visible corrosion has been reported in *Mercenaria mercenaria* after long periods of valve closure resulting from extended periods of anaerobiosis (Dugal 1939). The ability of *G. demissa* to respire anaerobically for extended periods of time has been described (Kuenzler 1961; Lent 1967, 1968, 1969), as has the relative increased efficiency, in this species, of some of the citric acid cycle enzymes in an anaerobic direction (Hammen and Lum 1966). The observed shell corrosion may well be a reflection of buffering of acidic end products from anaerobic metabolism during the colder months when oxygen transport into the cells should theoretically be reduced relative to that occurring at higher temperatures (Lange et al. 1972). Wilbur (1972) has suggested that during periods of "adverse environmental conditions", shell decalcification may predominate over growth. The gradation in fractured, as well as polished and etched, vertical shell sections of G. demissa nacreous laminae into fine-grained structures (suggestive of massive corrosion) instead of regular prisms (Fig. 12F) tends to support this view. As water temperatures increase during the spring, the sequence of events described above is reversed. Examination of growth surfaces during transition periods (spring and fall) between normal nacreous deposition (summer) and drastic corrosion (winter), reveals differential dissolution of calcium carbonate and organic material, with corroded aragonitic tablets above and below exposed sheets of interlamellar organic matrices (Fig. 13). Despite such shell dissolution, successive monthly samples often indicate a net gain of shell material during these "transition" periods. We therefore suggest that the observed growth surfaces are a reflection of alternating periods (not necessarily rhythmic) of shell deposition and destruction. Here, alternating periods of aerobic and anaerobic metabolism, respectively, which have already been demonstrated to occur in at least one species (M. mercenaria; Crenshaw and Neff 1969; Gordon and Carriker 1978), could easily provide the driving forces.

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[23] A similar irregularity of nacreous crystals as a result of dissolution during reduced winter temperatures (as low as 8°C.) was found by Wada (1912) in his examination of growth surfaces of *Pinctada martensii* and *Pinna attenuata*.

In the preceding paragraph, we have described changes occurring primarily on the growth surface itself. When the shell is viewed in section, using fracture, acetate peel, or thin section techniques (see Appendices 1 and 2), one is able to observe how these changes are recorded within the shell. Figures 12F and 15B depict, respectively, a fractured section and an acetate peel of a polished and etched longitudinal section of the inner layer of a G. demissa shell valve from the Gulf of Maine (Damariscotta River, Lincoln County, Maine). In these sections, one observes a gradation (progressing toward the inner shell layer growth surface) of nacreous laminae into a fine-grained "homogeneous" structure which gradually becomes increasingly coarse-grained and subsequently grades into simple aragonitic prisms. In turn, these simple prisms, which are strikingly similar in appearance to myostracal prisms, grade into nacreous tablets. It is also interesting to note that at the bottom of Figure 12F, the first few nacreous tablets appear to be stacked upon one another, while subsequently deposited tablets assume a more steplike (Treppen; see Schmidt 1923, and Wise 1970a, b) pattern. These repetitive changes result in a series of distinct sublayers within the inner shell layer of mature specimens.

We have described above the sequence of seasonally-related changes occurring on the growth surface and within the shell of G. demissa specimens from relatively cold-water (high latitude) environments. Seasonal changes occurring on the inner shell layer surface of specimens from warmer water environments (e.g. south of Cape Cod on the east coast of North America) are somewhat more complex. In these populations, one still sees alternating sublayers associated with cold-water shell deposition and dissolution, but one also encounters irregular prismatic sublayers which are associated with extremely warm summer temperatures (Lutz and Rhoads 1978). There irregular prismatic sublayers may be associated with the increased utilization of anaerobic pathways during the hot summer months when oxygen solubility is markedly reduced. However, in all of the specimens examined to date from south of Cape Cod (Lutz 1976b, 1977; Lutz and Rhoads 1978), we have never observed homogeneous structures in "warm-water" sublayers. This well may indicate decreased shell destructive processes at relatively high (relative to extremely low) temperatures. When viewed in longitudinal section, such complex seasonal variation often results in an alternation of three distinct types of sublayers within the inner layer: (1) irregular prismatic ("warm-water" sublayer); (2) homogeneous + irregular prismatic "cold-water" sublayer); and (3) nacre. These three types of sublayers are generally present in the majority of specimens sampled from relatively temperate environments (e.g. Cape Cod to Cape Hatteras) (Fig. 14, 15C). In sub-tropical environments (e.g. south of Cape Hatteras), homogeneous structures are absent, resulting in an alternation of only irregular prisms and nacre (Fig. 15D).

Structural patterns described in the above discussion are summarized in Figure 15. The micrographs in this figure depict acetate peels of the inner shell layer of G. demissa specimens from four geographically separated populations from Prince Edward Island to Florida. Marked differences in the percentages of various structural types are obvious.

The mechanism described above for the formation of structural changes has important implications. For example, in paleotemperature studies based on oxygen isotope analyses, it is important to realize that truncated seasonal paleotemperature curves may reflect a net loss of shell material during certain times of the year. Similarly, shell dissolution may account for certain apparent ontogenetic discontinuities in elemental (or chemical) distribution patterns within the shell of individual specimens. We hope that the implications of shell dissolution and redeposition discussed above will eventually result in the realization that the shell is far more than a simple accretionary deposit.

Documented Growth Patterns and Their Ecological, Paleoecological, and Phylogenetic Applications

In the previous section, we proposed a hypothesis for the mechanisms responsible for the formation of certain structural changes within the molluscan shell. At this point, it is important for the reader to realize that not all the patterns which will be discussed here necessarily reflect periodic or aperiodic respiratory changes. Alternate hypotheses for the formation of structural growth patterns do not exist.[24] The reader should also realize that relatively few studies have been conducted in which patterns of structural change within molluscan shells have been adequately documented and anlyzed. Thus, while it may appear that we have summarized the results of only a few relatively specific studies, we have, in fact, presented a comprehensive review of the status of current knowledge.

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[24] Sublayers of simple aragonitic prisms possibly result from temporary mantle attachment (Taylor et al. 1969). While this might be viewed as an alternate hypothesis of structural growth pattern formation, it may not be independent of the mechanisms outlined in this chapter. It is conceivable, for example,

In 1954, Lowenstam showed that the relative amount of aragonite and calcite composing the shells of certain molluscs can reflect environmental conditions at the time of shell formation. As aragonite and calcite are present in distinct structural units in molluscan shells (Bøggild 1930), the variation in shell mineralogy found by Lowenstam (1954) suggested to Dodd (1963, 1964) that variation in the structure of the shell should also occur. As a result, Dodd conducted two detailed studies of the effect of temperature on the shell mineralogy and structure of the Recent mytilid Mytilus californianus. Significant results obtained by Dodd (1963, 1964) for this species were as follows: (1) the percentage of aragonite in the shell varies with temperature; (2) the extent and development of the inner calcitic prismatic layer is strongly dependent on growth temperature; (3) wedges of nacreous structure which often project into the inner prismatic layer form annually, making age determination of the shell possible; (4) growth rates determined from these wedges are directly proportional to mean temperature of the growth locality; and (5) quantitative paleotemperature determination based on shell structure variation in this species is possible. Moreover, Dodd suggested that the shell structure of other species of molluscs, particularly those having shell composed of a combination of calcite and aragonite, could potentially be used for determining paleotemperatures.

Since Dodd's (1963, 1964) pioneering work, several workers have examined the effects of temperature (or latitude) on the shell structure of various species of bivalves. Blackwell et al. (1977) considered the possibility that the structure of the "middle" aragonitic prismatic layer of Geukensia demissa varied with latitude but concluded that the observed variation reflected sub-specific differences and not a climatic gradient coinciding with the geographical range of this species. More recently, however, Lutz (1976b, 1977) and Lutz and Rhoads (1977, 1978) have shown that the structure of the inner

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that mantle attachment itself may be a direct consequence of anaerobiosis. Personal observations on Arctica islandica specimens which have been kept for extended periods of time under anoxic conditions, have suggested that the entire surface of the mantle inside the pallial line may be attached to the shell during anaerobiosis. If this is indeed the case, the entire surface of the mantle might be acting, during such periods, as a "muscle" which attaches the shell to the soft tissues. If so, the genetic term "myostracal prisms," which has been used by Taylor et al. (1969, 1973), may well appropriately characterize simple prisms occurring within sublayers in the inner shell layer of this (see Fig.   ), and other, species of molluscs. Before the term "myostracal prisms" can be employed, however, it must be demonstrated that the entire mantle surface can be appropriately termed a "muscle;" until evidence for this is provided, it is probably best to refer to such simple aragonitic prisms as "myostracal-like prisms.

shell layer of this species varies with both season and latitude. The extent of this variation can be seen in Figure 15. It should be apparent from a close examination of the micrographs in this figure that there is a relatively sharp decrease in the percentage of homogeneous structure with decreasing latitude (or increasing mean temperature). In light of this, it may eventually be possible to develop a quantitative approach [similar to that developed by Dodd (1964) for *M. californianus*] for the analysis of growth patterns within the shells of *G. demissa* and other closely related Recent and fossil species. Such an approach may prove useful in ecological studies for defining the effect of thermal stress gradients (e.g. power plant waste heat gradients) on bivalve shell growth and in paleoecological studies for defining both spatial and temporal paleotemperature patterns. Furthermore, analysis of structures adjacent to the inner shell layer surface of *G. demissa* from death assemblages[25] should prove useful in ecological, paleoecological, and archeological studies for defining the season of death of individual speciments (Fig. 16).

Other studies in which structural changes have been observed to be associated with thermal stress include those of Kennish and Olsson (1975), Kennish (1976, 1977a, b, 1978; see also Chapter 3), and Farrow (1972). In their studies of the effects of thermal discharges on the microstructural growth and mortality of *M. mercenaria*, Kennish and Olsson (1975) and Kennish (1976, 1977a, b, 1978) found that "crossed lamellar structure"[26] replaced prismatic structure in the outer shell layer of this species throughout the duration of high temperature stress periods. Farrow (1972) reported a somewhat similar phenomenon in *Cerastoderma edule*, in which a greater prominence of "crossed lamellar structure" in the outer shell layer was observed to be associated with winter reduction in growth rate. Farrow further observed that the lamellae became "markedly deflected" if an actual "stoppage" of growth took place.

Bryan (1969) described drastic changes within the shell of the gastropod *Nucella lapillus* which occurred subsequent to addition of oil-spill removers ("detergents") to the organisms' natural environment (following a large spill of Kuwait crude oil). When *N. lapillus* shells were sectioned longitudinally or transversely, it was found that "the shell edges had often been temporarily sealed by continuing the inner nacreous layer of the shell to the outer surface. Later growth of the shell was laid down on this nacreous layer partition and this produced a growth mark and a line of weakness in the shell" (Bryan 1969, pp. 1074-1075).

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[25] In analyzing the shells of specimens from death assemblages, one needs to distinguish post-mortem shell dissolution from shell dissolution which occurred while the organism was alive and respiring anaerobically. In the case of *G. demissa*, this is readily done by comparing growth surfaces of shell layers on either side of the pallial line. During anaerobiosis, shell structural changes in this species are apparent only within that portion of the shell inside the pallial line; evidence of dissolution of nacre on both sides of the pallial line (i.e. in both the middle nacreous layer and the inner layer of the shell) would indicate post-mortem diagenesis.

[26] The "crossed lamellar structure" described by the workers and by Farrow (1972) in the outer shell layer of *Mercenaria mercenaria* and *Cerastoderma edule* may merely represent a disordered arrangement (with a high organic content) which resembles (superficially?) crossed lamellar structure when viewed in acetate peel and thin section preparations (G. R. Clark, personal communication; R. A. Lutz, personal observation).

Many of the studies in which shell structural changes have been documented have been primarily concerned with the usefulness of observed growth patterns for determining the age of examined specimens. Weymouth (1923) commented on the presence of "translucent regions" within the inner shell layer of *Tivela stultorum* and provided evidence that such regions were formed with an annual periodicity (during winter) and, hence, could be of value in estimating the age of individual specimens. More recently, Rhoads and Pannella (1970) have demonstrated the annual nature of pigmented growth bands within the inner "homogeneous" layer of the hard shelled clam, *M. mercenaria*. Similar annually-formed pigmented bands have been found by Jones et al. (1978) within the inner shell layer of *Spisula solidissima* and were used by these workers to determine the age and growth rate of this species in both inshore and offshore populations. Lutz (1976a) has presented evidence that structural patterns within the inner nacreous layer of *Mytilus edulis* reflect annual cycles of growth and has suggested that careful examination of these patterns can provide a relatively accurate estimate of the age of individual mussels (Fig. 17). The ultrastructure of the patterns described by Lutz (1976a) is shown in Figure 18. Relatively thick aragonite crystalline laminae abruptly decrease in size to form a zone of fine laminae which gradually increase in thickness toward the inner shell surface. It is interesting to note that the zone of fine laminae were observed to form only during the spring of each year when water temperatures were rising (Fig. 18C). If, as suggested by Lutz (1976a), the thickness of nacreous laminae is temperature-dependent, one would expect to observe within the shell a *gradual* decrease in the thickness of nacreous tablets rather than the abrupt decrease seen in Figure 18A, C. We suggest that the observed structural patterns within *M. edulis* may reflect anaerobiosis-related shell dissolution during the late winter and early spring (perhaps related to gametogenesis). If shell destructive processes are indeed operating during this period, nacreous laminae may actually be destroyed, and one would expect to only encounter relatively thick, previously deposited nacreous laminae at the inner shell surface (e.g. Fig. 18B). With increased utilization of aerobic pathways during late spring, net shell growth takes place, albeit perhaps irregularly at first, resulting in the formation of thin, irregular nacreous laminae which gradually increase in thickness (Fig. 18C, D) as anaerobic pathways are employed less and less. Patterns morphologically very similar to those described above in *M. edulis* have been found by Hudson (1968; personal communication)[27] within the inner shell layer of the Jurassic mytilid Praemytilus strathairdensis. Hudson (1968) speculates on the annual origin of these "sub-layer junctions." If such patterns are indeed analogous to those encountered within M. edulis, they should be of considerable assistance in reconstructing growth rates of P. strathairdensis in various paleoenvironments. Finally, Wada (1961, 1972) has commented on the presence of somewhat similar structural changes in various bivalves (particularly Pinctada). He comments on seasonal variations in the size of aragonite crystals, as well as the effects of extrapallial fluid pH, viscosity, and impurities on nacre tablet size, shape, and texture.

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[27] In his paper, Hudson (1968, p. 173), in referring to "sub-layer junctions" within the inner nacreous of *Praemytilus strathairdensis*, states that aragonite laminae "tend to grade into those above (i.e. older), and have a sharp junction with those below." Plate 33, Fig. 2 of his paper, however, shows

In the remainder of this chapter, we would like to discuss briefly several of the phylogenetic and paleoecologic implications of our ideas on the relationship between bivalve metabolism and shell structure. For purposes of illustration, we will discuss many of the implications in light of the patterns described above within the shell of G. demissa.

It has been proposed that the stacked "mode of deposition" of nacre is a primitive trait among molluscan species which has been lost by degrees in bivalves during their evolution of a "new (bivalve) shell form" (Wise 1970a,b). More recently, Taylor (1973, personal communication) has suggested that the "vertical component" of nacre is more closely related to geometry of the shell rather than the antiquity of the lineage, arguing that bivalves with low expansion rates (high convexity) have better developed stacked nacre than forms with high rates of expansion. One may alternatively view the various configurations of nacre within the bivalve shell as reflecting changing metabolic pathways (Lutz and Rhoads 1977). Assuming that atmospheric oxygen levels increased from the late Precambrian to present levels in the Ordovician (Berkner and Marshall 1965; Cloud and Nelson 1966; Brinkman 1969; Rhoads and Morse 1971; Crimes 1974), we suggest that aerobic respiration progressively increased over this same period of geologic time and resulted in an increased shell deposition to shell dissolution ratio and, hence, increased proportions of sheet nacre (see Appendix 2B)[28] in certain bivalves. Moreover, in G. demissa, during "transition" periods described in the previous section,

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just the reverse, with crystalline laminae grading into those below (i.e. younger) and having a sharp junction with those above. In personal communications (see Lutz 1976a), Dr. Hudson has indicated that the text statement is in error and that the structural patterns within the inner shell layer of P. strathairdensis are very similar to those found within the shells of M. edulis.

[28] Schmidt (1923) used the terms Backsteinbau, Treppen, and Vertikalschichtung for, respectively, brick-wall, stepped, and columnar (or lenticular) patterns of nacre (see also Lutz and Rhoads 1977). Schmidt's terms were defined by him (and are used by most workers) in only two dimensions. One may alternatively classify the stacking modes of nacre according to a three-dimensional scheme. "Sheet" nacre includes Backsteinbau and Treppen in various vertical two-dimensional views. "Row stack" nacre appears as Backsteinbau or Treppen in some vertical two-dimensional views, and as Vertikalschichtung in others. Finally, "columnar" nacre appears as Vertikalschichtung in all vertical two-dimensional views.

increased stacking of crystals[29] actually results in structural changes, during which nacre subtly grades into simple aragonitic prisms, or the reverse (Figs. 12F, 13). Physiological and/or other mechanisms responsible for the increased stacking of nacreous tablets (i.e. increased proportions of columnar nacre) and for this gradation of nacre into simple prisms warrants additional research.[30] Similar bands of simple aragonitic prisms are found alternating with complex crossed lamellar and homogeneous structures within the inner shell layer of *Arctica islandica* (Fig. 19), an organism known to respire anaerobically during extended aperiodic burrowing activities (Taylor 1976).[31] This suggests that such aragonitic prisms may represent a shell microstructure that reflects low oxygen environments. Such a view is compatible with the phylogenetic tree presented by Taylor et al. (1973) in which the relationships between bivalve superfamilies, their possible history, and their shell structures have been summarized. The earliest ancestral forms in which shell structures can be recognized are composed of nacre and simple prisms of aragonite. It has been suggested (Taylor 1973) that the simple prism and nacre combination originally arose spontaneously as a consequence of the precipitation of calcium carbonate contemporaneously with organic matrix under a certain set of physicochemical conditions. Subsequently, because of some selective advantage in this structural combination (Taylor and Layman 1972), this condition became stabilized. In the above discussion, we imply that simple aragonitic prisms represent an altered form of nacre resulting from alternating processes of shell deposition and dissolution. Assuming this to be the case, we suggest that the evolutionary scheme proposed by Wise (1970a, b) be extended backward one step. We propose a gradual change (not necessarily evolutionary in a genetic sense) within certain ancestral molluscan lines from simple aragonitic prisms to columnar [*Vertikalschichtung* of schmidt (1923)], then row stack, and finally, sheet [Treppen and Backsteinbau of Schmidt (1923)] nacre. It is also interesting to note that, if such structural changes have occurred, aragonitic (myostracal) prisms associated with the sites of muscle attachment may represent vestiges of an early ancestral shell structure. Inasmuch as such structural changes may be correlated with oxygen tension, a detailed analysis of relationships between ambient oxygen concentrations and various shell structural types within certain Recent and fossil molluscan superfamilies may eventially prove useful in determining dissolved oxygen gradients in present, as well as ancient, marine environments (Lutz and Rhoads 1977).

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[29] A similar stacking of nacreous tablets may be seen in micrographs presented by Wise (1970b) of the surfaces of *Pinna carnea* and *Nucula annulata*. *Nucula annulata* = *Nucula proxima*; Hampson (1971).

[30] Similar structural changes (i.e. sublayers of simple aragonitic prisms) within the shells of numerous molluscs, such as the Pennsylvanian gastropod *Shansiella carbonara* (Batten 1972), the Jurassic bivalves *Lithiotis problematica*, *Cochlearites loppianus*, and *Lithiopedalion* sp. from the "Lithiotis" facies (Loriga and Neri 1976; Benini and Loriga 1977; Benini, personal communication), the Recent bivalves *Modiolus modiolus*, *Cyclinella saccata*, and *Pholadomya candida* (Taylor et al. (1969, 1973), and numerous species within the superfamily Chamacea (Kennedy et al. 1970), may result from periods of anaerobiosis.

[31] Thompson and Jones (1977) have recently suggested that these bands of simple aragonitic prisms may occur with an annual periodicity. These workers have arrived at age estimates, based on counts of such "annual" bands, as high as 150 years for certain specimens. If these simple prismatic sublayers are related to the aperiodic burrowing activity of this species, such estimates may be unrealistically high.

ACKNOWLEDGMENTS

We thank G. R. Clark II, G. D. Rosenberg, G. Pannella, J. G. Carter, and M. J. Kennish for discussions and critical reviews of the manuscript; M. Castagna, J. N. Kraeuter, M. D. Bertness, D. K. Muschenheim, J. G. Carter, and A. Sesona for sampling specimens of *Geukensia demissa*; W. C. Phelps, P. Duckett, K. Genthner, V. Clark, and R. Noddin for preparation of specimens; W. K. Sacco and R. D. Smith for assistance with photographic reproductions; A. S. Pooley and E. Tveter Gallagher for technical assistance with the scanning electron microscopy; and S. E. Hurlburt for many heartfelt smiles. Much of the research summarized in this chapter was supported by Environmental Protection Agency grant R804-909-010 and NOAA Sea Grants 04-6-158-44056, SGI-77-17, and 04-7-158-44034.

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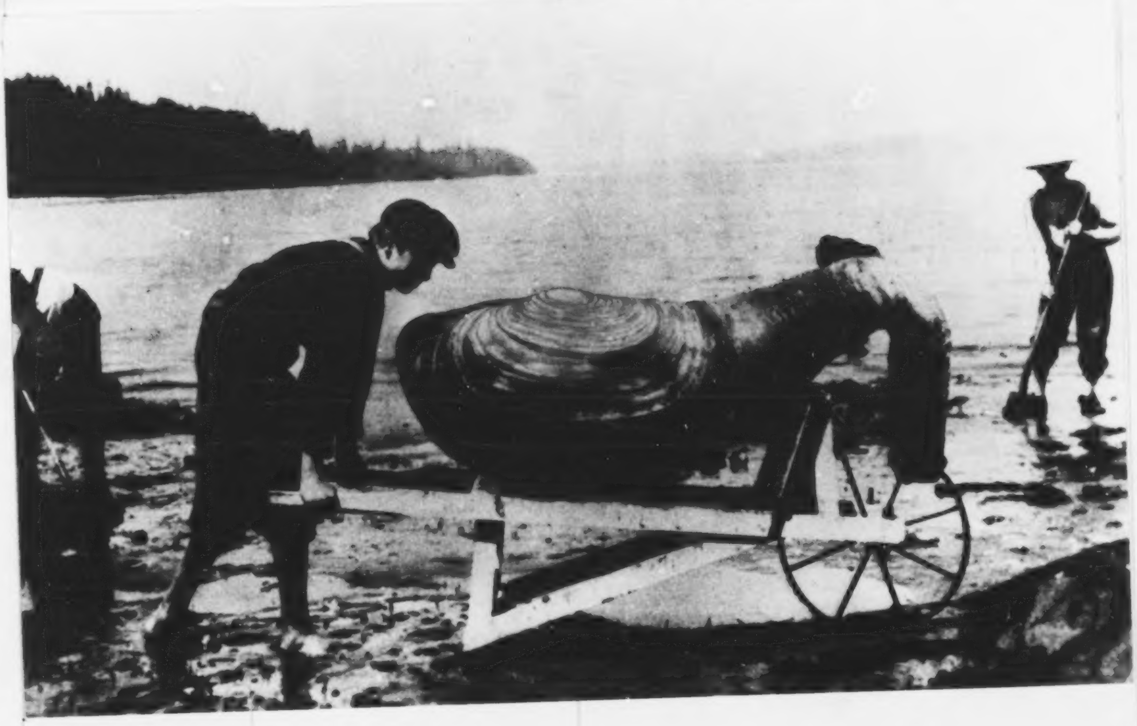

Fig. 1. The geoduck, Panope generosa (Gould). Distinct growth patterns are visible on the external surface of the shell. Note wheelbarrow for scale. Origin of photograph unknown.

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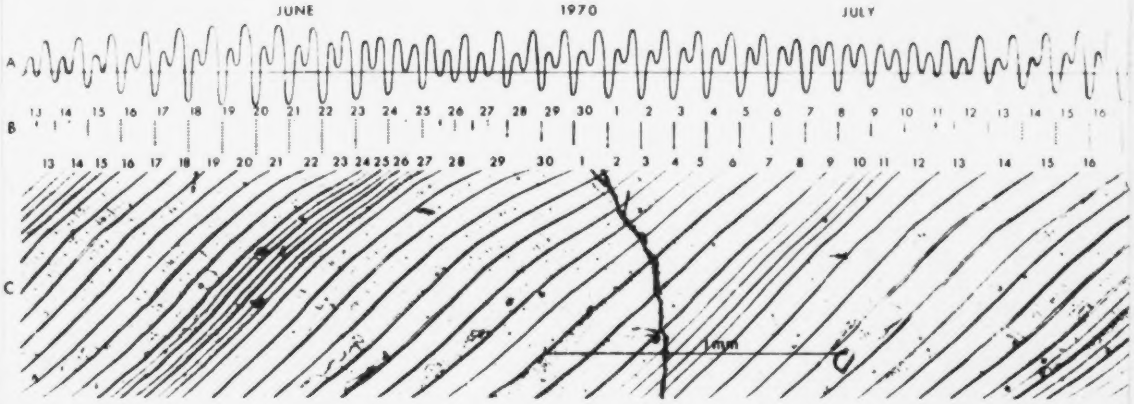

Fig. 2. Microgrowth increments in the outer shell layer of the intertidal cockle *Clinocardium nuttalli* collected at Charleston, Oregon, compared with tidal predictions for the same period for Empire, Oregon. The horizontal line drawn through the tidal curves marks the intertidal position at which the specimen was collected. The optical micrograph is of an acetate peel of a polished and etched, radially sectioned shell valve. Diurnal, semidiurnal, and fortnightly patterns are apparent. Slightly modified from figures which appeared in Evans (1972) and Clark (1974). Reprinted with permission.

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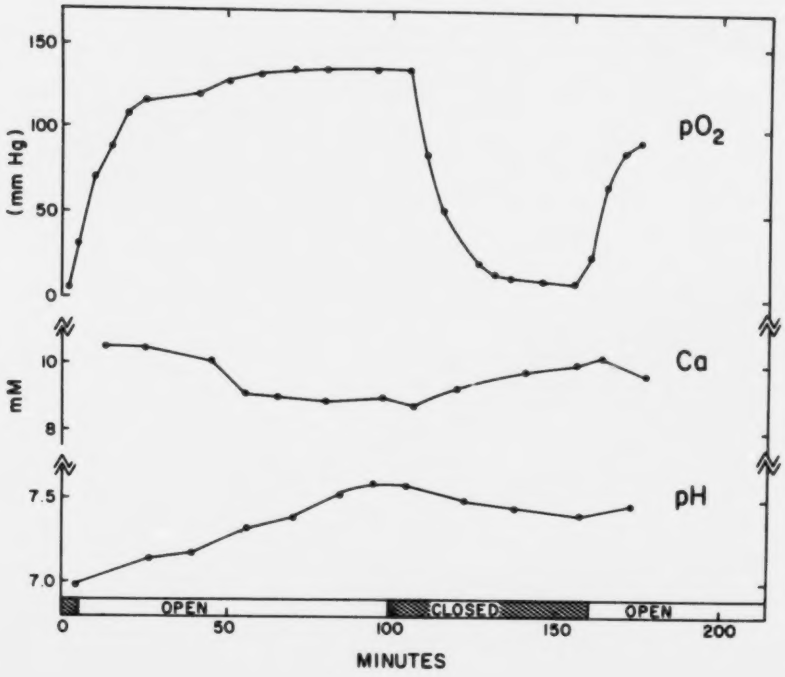

Fig. 3. The oxygen tension (pO_2), calcium (Ca) concentration, and pH of the extrapallial fluid of one *Mercenaria mercenaria* specimen with respect to the opening and closing of the shell valves. Valve position is indicated by the bar at the bottom of the graph. Reprinted with permission from Crenshaw and Neff (1969).

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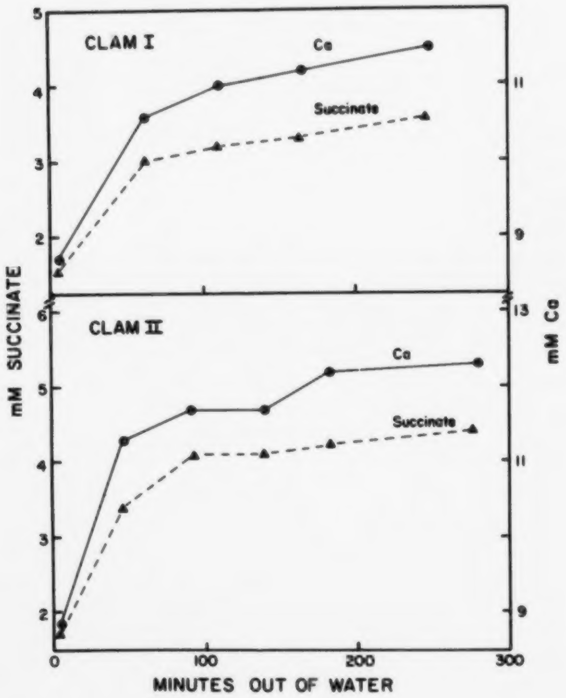

Fig. 4. The concentration of calcium and succinate in the extrapallial fluids of two clams (Mercenaria mercenaria) with respect to time out of water. Reprinted with permission from Crenshaw and Neff (1969).

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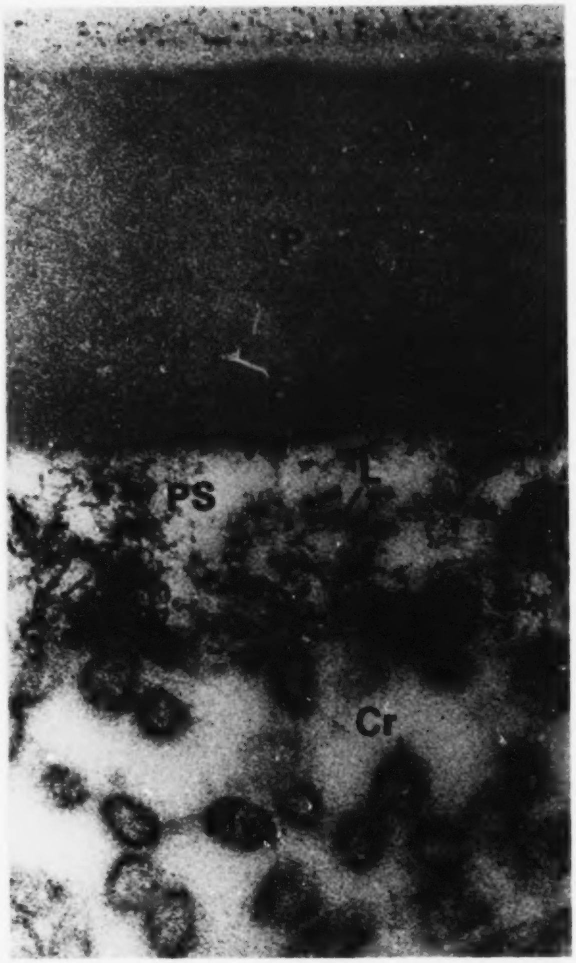

Fig. 5. Electron micrograph of a vertical section of the pallial region of Pinctada radiata. The live specimen was relaxed in a solution of magnesium sulphate prior to fixation in glutaraldehyde and osmium tetroxide. Calcium carbonate crystals (Cr) and fragments of "electron-dense lamellae" (L.) are seen scattered throughout the pallial space (Ps). P, periostracum; Mv, microvillae of mantle cells. Unstained section x110,000. Reprinted with permission from Nakahara and Bevelander (1971).

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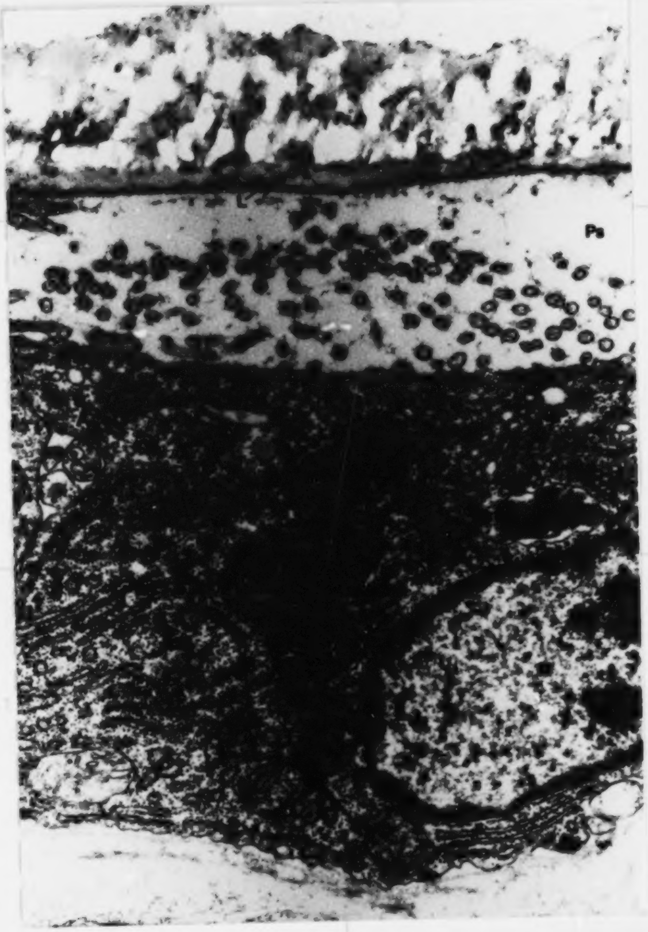

Fig. 6. Electron micrographs of the pallial region of Pinctada radiata. The live specimens were relaxed in a solution of magnesium sulphate prior to fixation in gluteraldehyde and osmium tetroxide. All sections have been stained with uranyl acetate and lead citrate. (A) Vertical section of a mantle cell (bottom of micrograph), pallial space (Ps), lamella (L), and portion of a prism (Pr). This region was located proximal to the outer fold of the mantle x27,000. (B) Vertical section in a region of pallial space showing a portion of a prism (PR) containing scattered calcium carbonate crystals (Cr), interprismatic wall (IW), lamella (L), and tips of microvillae (Mv). Decalcified section x76,000. (C) Vertical section of mantle cells (bottom of micrograph), pallial space, lamella (L), and portion of three prisms. Microvilli of mantle cells extend into the pallial space. The prisms are separated from one another by substantial interprismatic walls (IW); "intraprismatic organic strands" (Is), and "remnants of envelopes and ground substance" (Nakahara and Bevelander, 1971) are seen between the walls. Decalcified section x6700. All micrographs reprinted with permission from Nakahara and Bevelander (1971).

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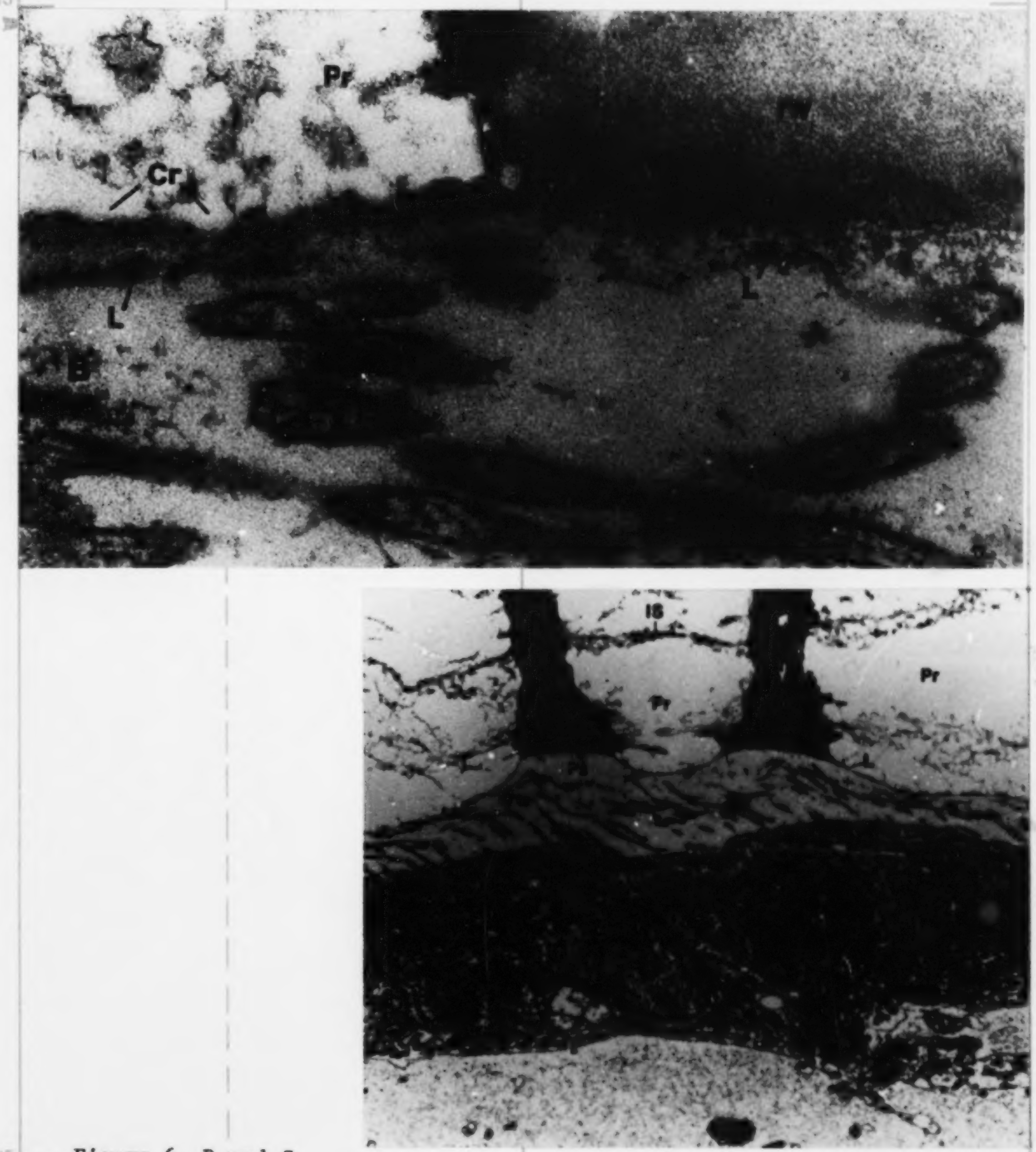

Figure 6. B and C

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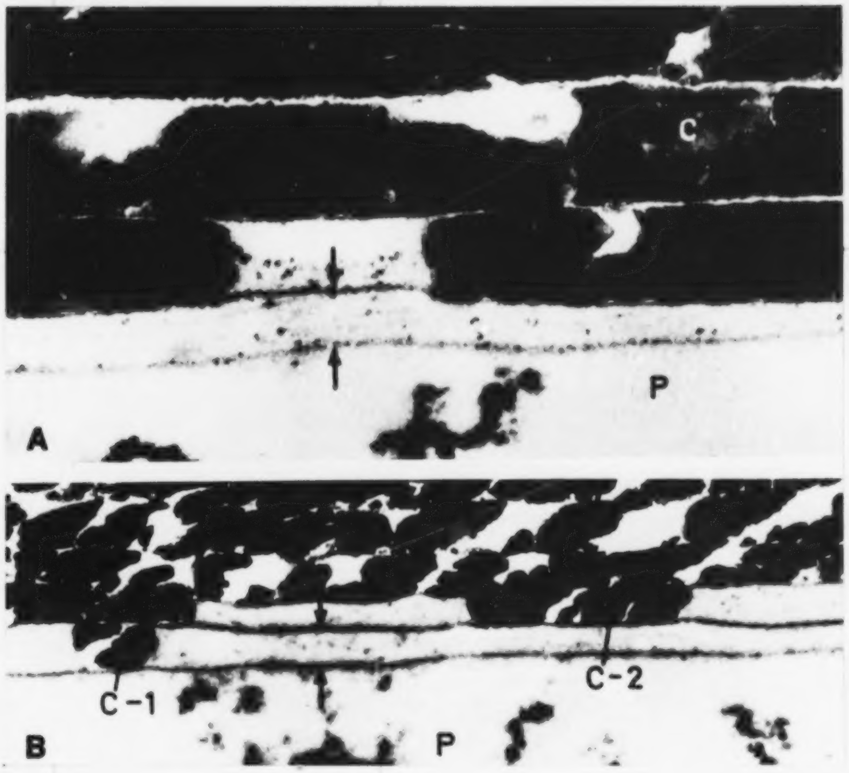

Fig. 7. (A,B) Electron micrographs showing portions of the pallial space (P) and formed shell (C) of Mytilus exustus. The live specimens were placed in a refrigerator at 5°C for 1 hour prior to fixation in glutaraldehyde and osmium tetroxide. Such pre-fixation treatment may have induced anaerobiosis, with release of succinic acid into the extrapallial fluid. "Compartments" are delimited by organic lamellae (arrows). C-1, C-2, incomplete (partially dissolved?) aragonitic tablets in adjacent nacreous laminae. (A) x46,000. (B) x20,000. Both micrographs reprinted with permission from Bevelander and Nakahara (1969).

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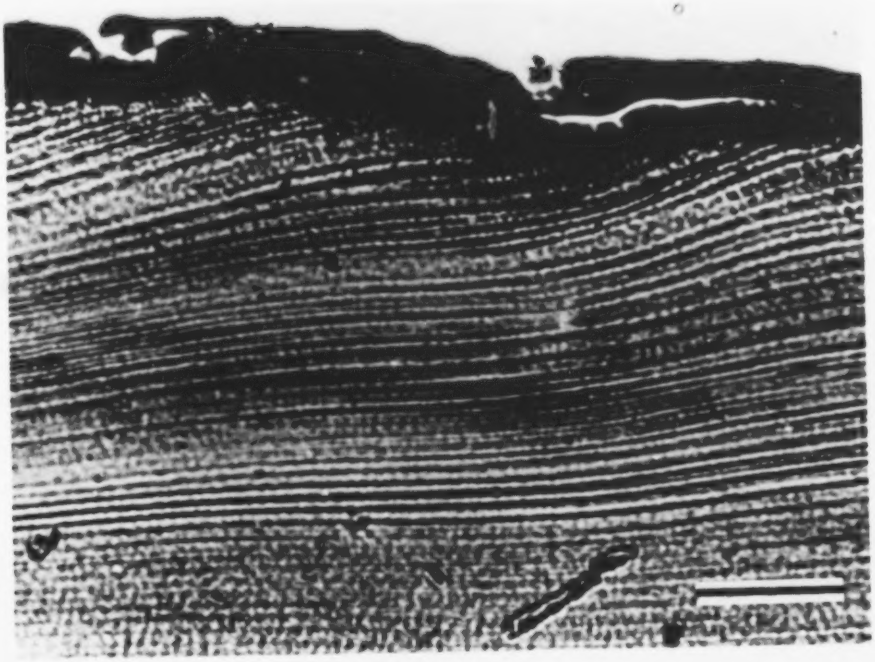

Fig. 8. Optical micrograph of an acetate peel of a polished and etched longitudinal shell section showing nonreflected growth lines within the middle nacreous layer of Geukensia demissa. Note the pronounced clustering of microgrowth increments. Scale bar equals 100 μm. Reprinted with permission from Lutz and Rhoads (1977).

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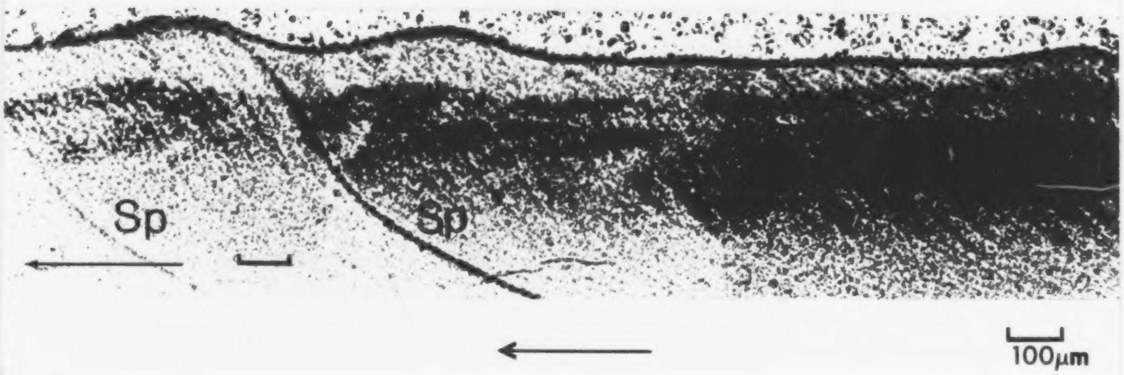

Fig. 9. Optical micrograph of a thin section of the outer shell layer of Malletia sp. from 4970 meters on the lower continental rise. Two major breaks in shell deposition have been interpreted by Rhoads and Pannella (1970) to mark spawning events (Sp). Arrow indicates direction of growth. Thin section YPM-IP 28157. Reprinted with permission from Rhoads and Pannella (1970).

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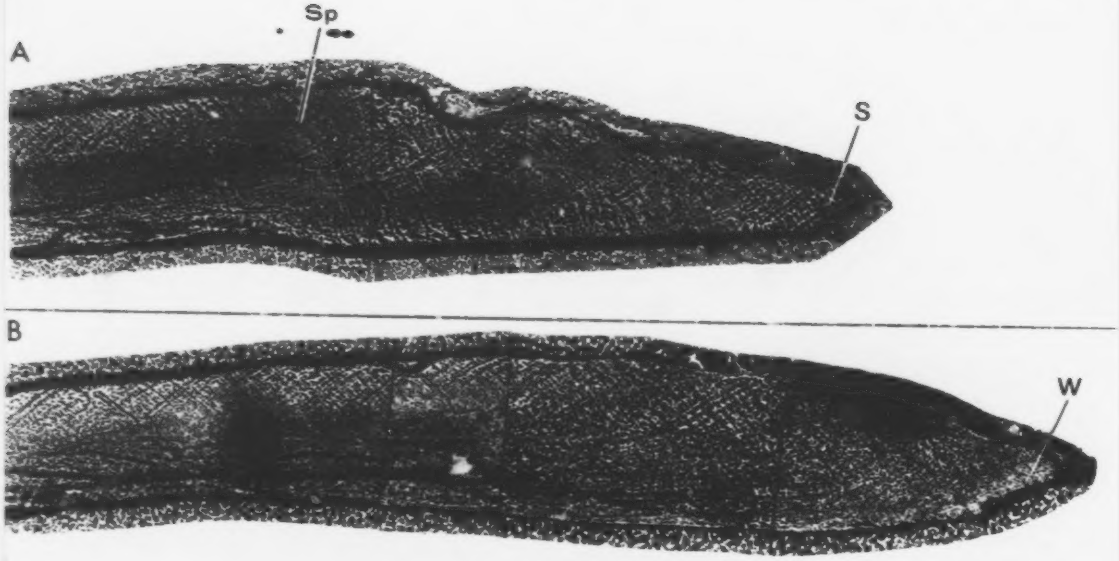

Fig. 10. Summer and winter death recorded in microgrowth patterns of Gemma gemma Totten. Both A and B depict optical micrographs of acetate peels of polished and etched shell sections. (A) Summer death (S). The shell edge is preceded by relatively large increments characteristic of summer growth. In the earlier part of the shell the thin increments are probably related to spawning (Sp). Acetate peel YPM-IP 28158. (B) Winter death (W). The shell edge is preceded by thin increments marking a period of slow growth. Thicker bandings in the early part of the shell mark the preceding summer's growth. Acetate peel YPM-IP 28163. Reprinted with permission from Rhoads and Pannella (1970).

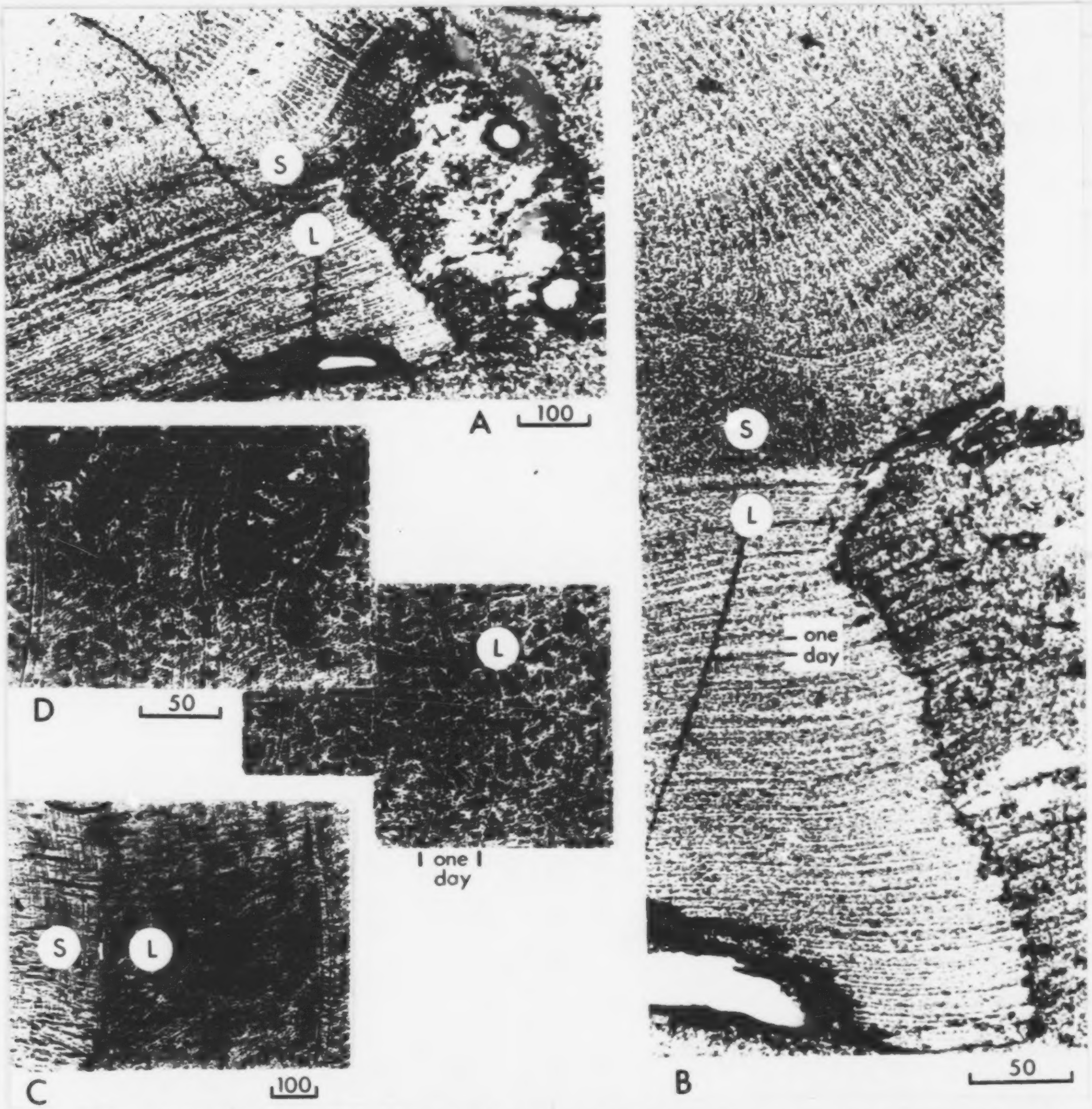

Fig. 11. (A) Acetate peel of an Astarte castanea Say specimen transplanted from a subtidal environment (S) to a laboratory holding tank without substratum (L). Periostracal extensions and changes in shell structure and growth rate mark the transplant event. (B) Enlargement of A. A daily growth increment is shown. Acetate peel YPM-IP 28159. (C,D) Acetate peels of a Mercenaria mercenaria (Linnaeus) specimen transplanted from a subtidal environment (S) to a laboratory holding tank without substratum (L). (C) Changes in shell structure and growth rate mark the transplant event. (D) Enlargement of periostracal extensions showing a large daily growth increment. Acetate peel YPM-IP 28161. Reprinted with permission from Rhoads and Pannella (1970).

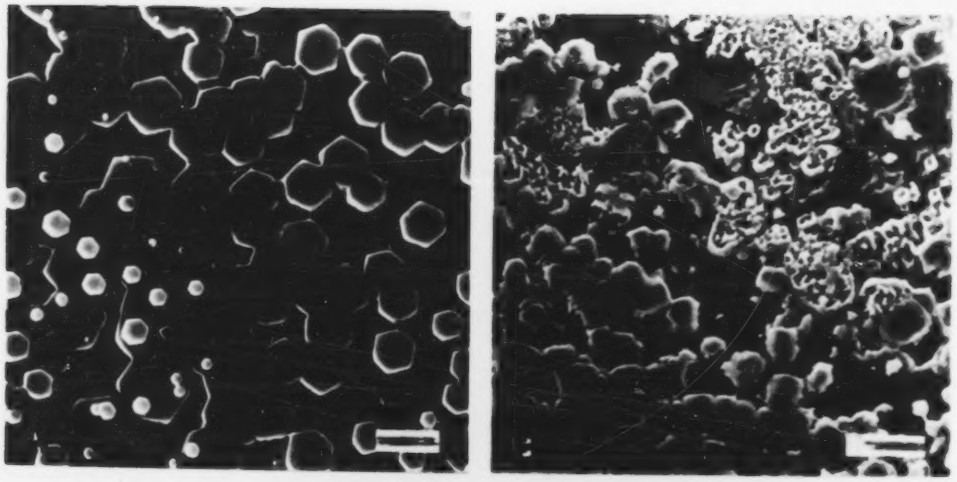

Fig. 12. (a & b) Scanning electron micrographs of Geukensia demissa (Dillwyn). (A-E) Inner shell layer growth surface as seen during various months of the year. (A) Regular hexagonal nacreous tablets arranged in steplike patterns characteristic of bivalve nacre (August sample). Scale bar equals 10 µm. Small, irregular nacreous tablets showing visible signs of corrosion in the form of marked pittings and increased proportions of fine-grained structures (November sample). Scale bar equals 5 µm. (C,D) Extremely irregular nacreous tablets with considerable amounts of fine-grained structures (December sample). The stereo pair was taken with a 6° angular displacement between exposures. Scale bar equals 10 µm. (E) Fine-grained structures reflective of extensive shell dissolution during the colder months of the year (February sample). Scale bar equals 10 µm. (F) Vertical fracture through the inner shell layer. Nacreous tablets grade into fine-grained structures at the top of the micrograph and the prisms grade into nacre at the bottom. The most recently deposited crystals are at the bottom of the micrograph. Scale bar equals 10 µm. Micrographs A,B,E, and F reprinted with permission from Lutz and Rhoads (1977).

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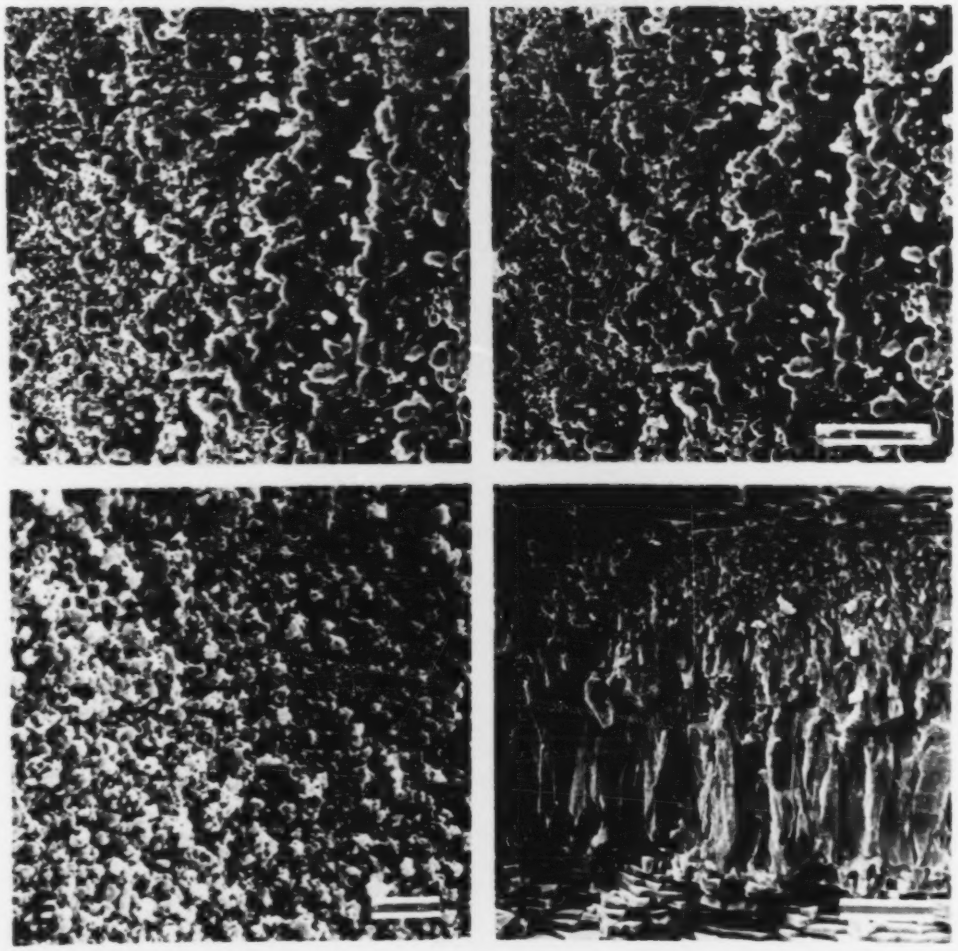

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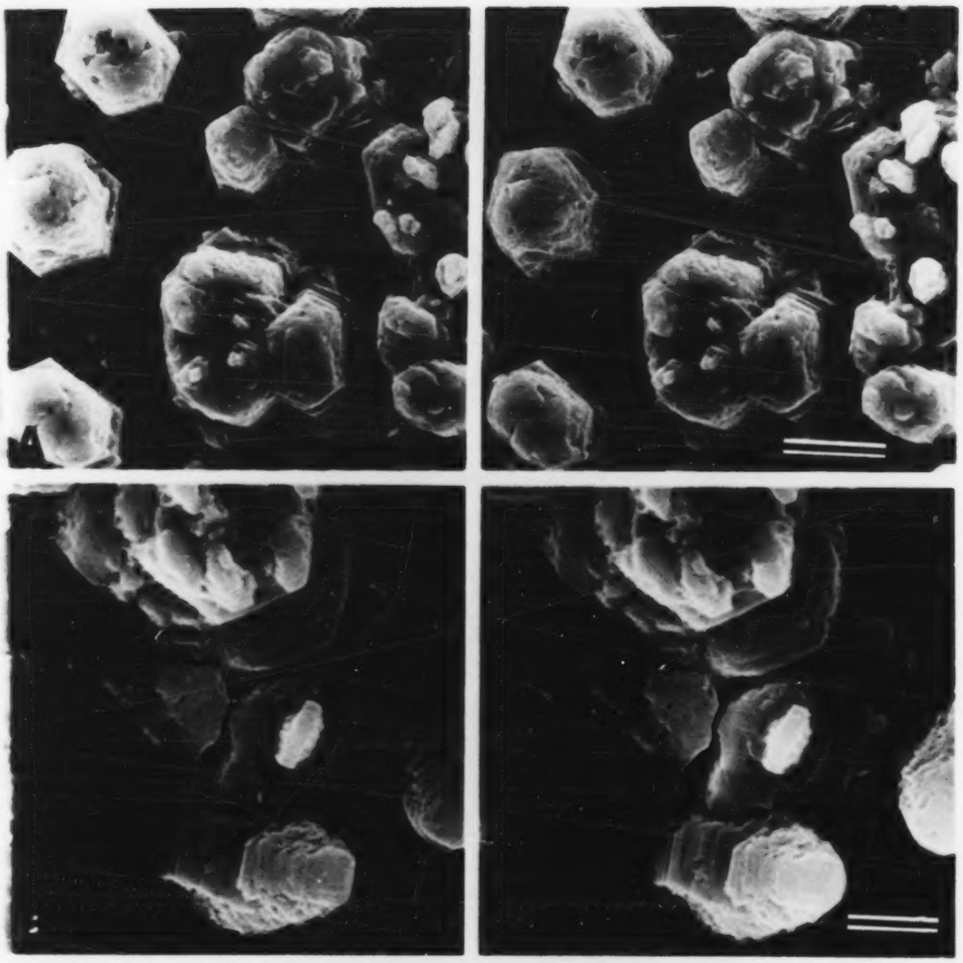

Fig. 13. (a & b) Scanning electron micrographs of the inner shell layer growth surface of Geukensia demissa (Dillwyn) showing natural shell dissolution. Stereo pairs were taken with a 6° angular displacement between exposures. Note the marked pitting and stacking appearance of nacreous tablets. The differential solubility of calcium carbonate and organic matrices is apparent. Scale bars are as follows: (A) 5 μm; (B) 2 μm; and (C) 1 μm. Reprinted with permission from Lutz and Rhoads (1977).

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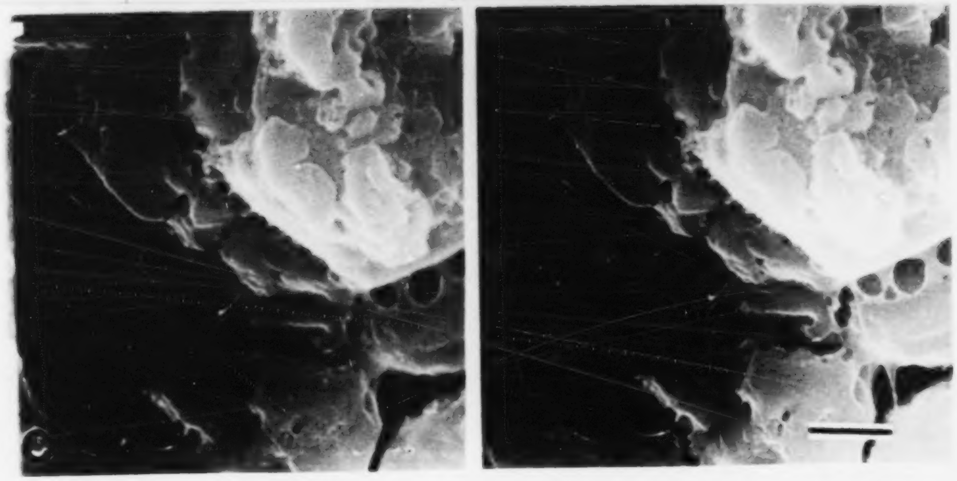

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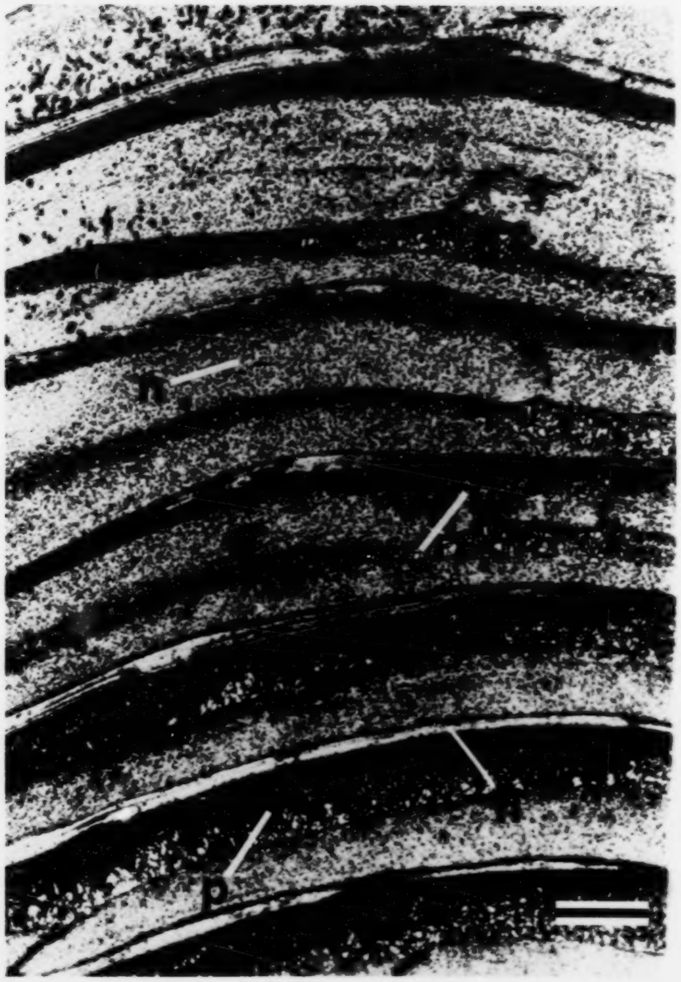

Fig. 14. Optical micrograph of a polished and etched antero-posterior longitudinal section of a Geukensia demissa shell from Wachapreague, Virginia. The micrograph is taken in the region of the umbo. Three types of sub-layers are apparent: (1) nacre (n); (2) irregular prismatic (p); and (3) irregular prismatic (p) + homogeneous (h). Note the decreased percentage of nacre in the most recently formed regions (bottom of micrograph) of the shell. Scale bar equals 100 μm.

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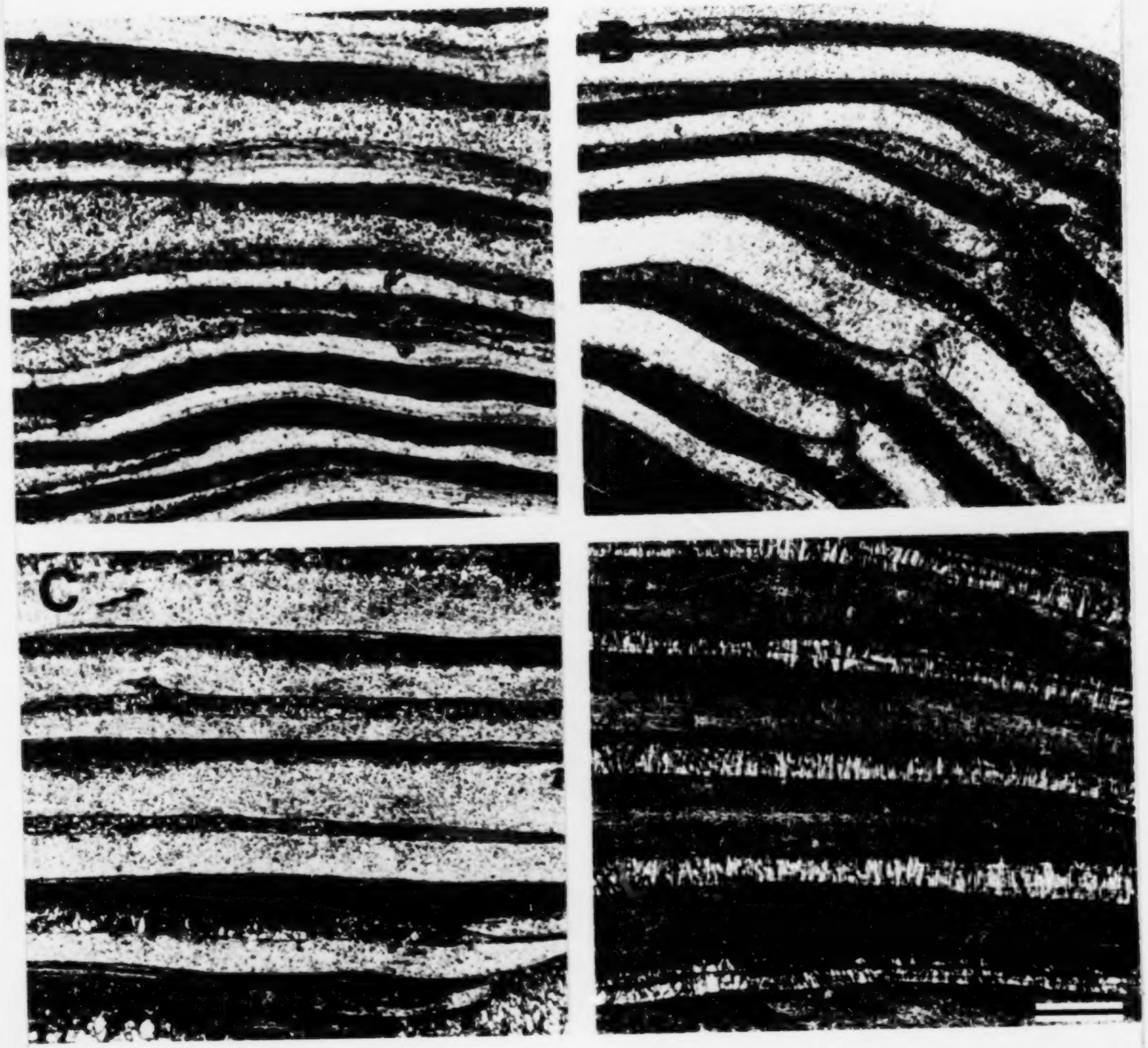

Fig. 15. Acetate peels of polished and etched antero-posterior sections of the inner shell layer of Geukensia demissa (Dillwyn) specimens from four latitudinally-separated populations. All micrographs were taken in the region of the umbo. The direction of growth is toward the left. (A) Specimen sampled from St. Peter's Bay, Prince Edward Island. (B) Specimen sampled from the Damariscotta River, Lincoln County, Maine. (C) Specimen sampled from Wachapreague, Virginia. (D) Specimen sampled from Cape Kennedy, Florida. Scale bar equals 100 μm and is for all four micrographs.

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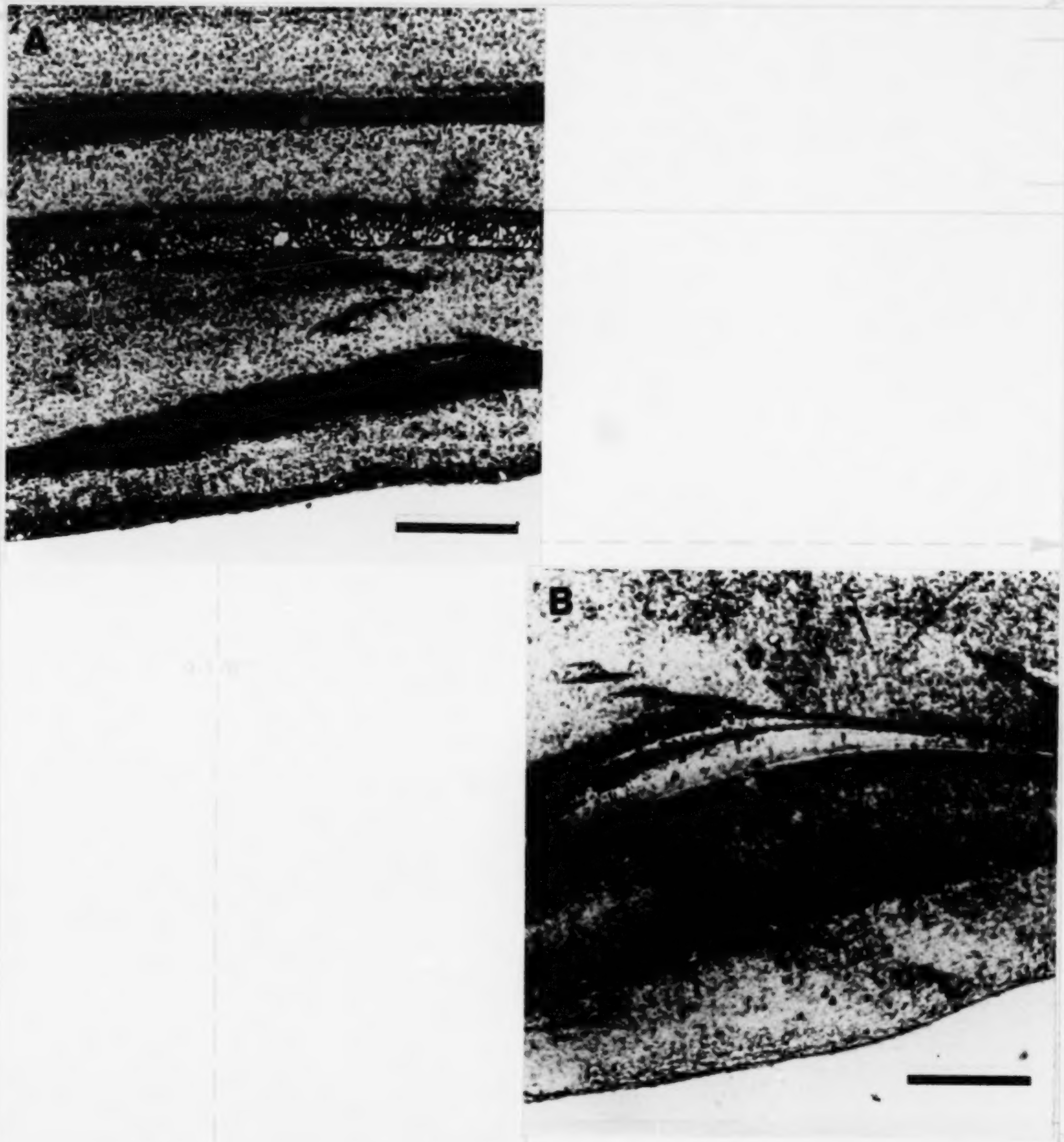

Fig. 16. Optical micrographs of acetate peels of polished and etched anteroposterior longitudinal sections of Geukensia demissa (Dillwyn) shells sampled at different times of the year. Examination of structures adjacent to the inner shell layer surface should prove useful for defining the season of death of individual specimens. (A) Specimen sampled on August 4, 1976 at Wachapreague, Virginia. Note irregular prismatic structure at the growth surface (bottom of micrograph). Scale bar equals 50 μm. (B) Specimen sampled during mid-October at Crisfield, Maryland. Note nacre at the growth surface (bottom of micrograph). Scale bar equals 50 μm.

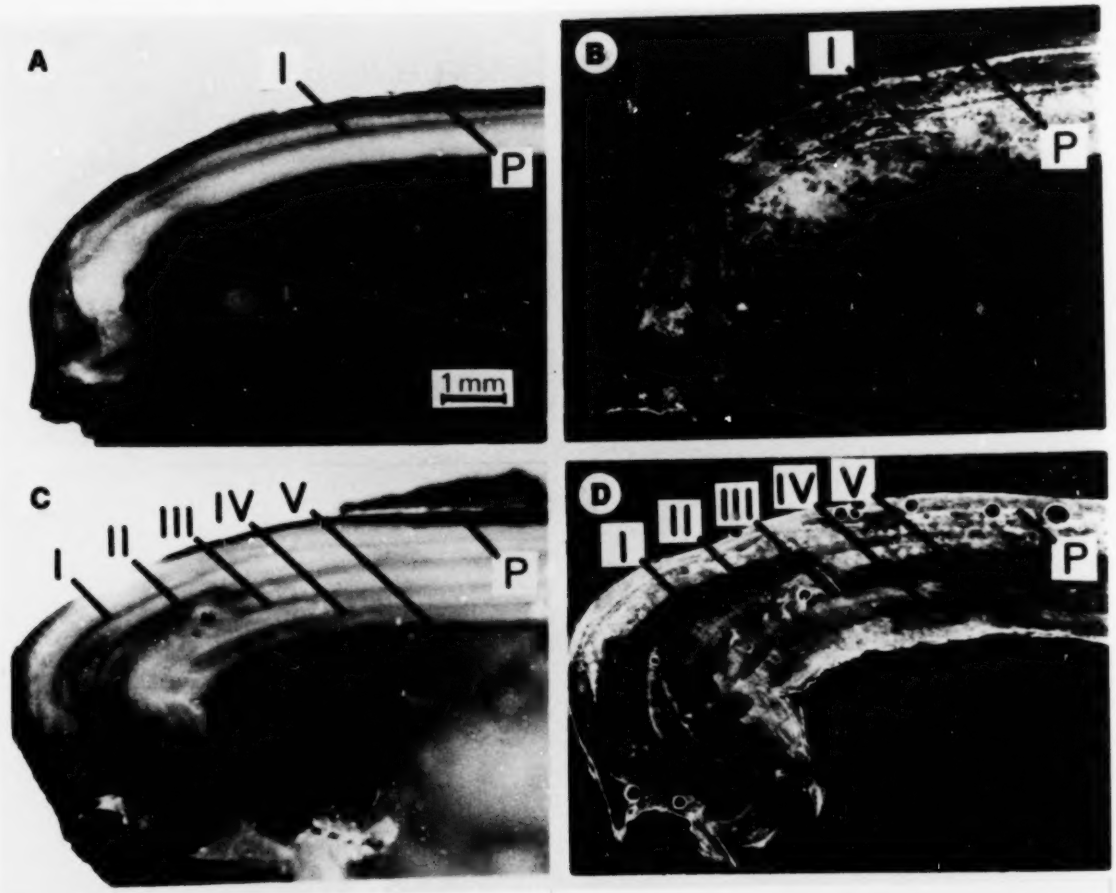

Fig. 17. (a, b, c & d) Finely polished and etched antero-posterior longitudinal shell sections (left) of Mytilus edulis L. with corresponding acetate peels (right). Roman numerals designate annual growth patterns. Scale for all shell sections is depicted in (A). All specimens were sampled from the Damariscotta River, Lincoln County, Maine. (A) 1½-year-old specimen from a constantly submerged (rafted) population (larval settlement: May, 1971; sampling date: 4 January, 1973). (B) Acetate peel of umbonal region of (A). (C) Specimen sampled from a constantly submerged population on the underside of a floating platform which was launched in July, 1967 (sampling date: 4 August, 1972). (D) Acetate peel of umbonal region of (C). (E) Specimen sampled from an intertidal population during the month of November. (F) Acetate peel of umbonal region of (E). Reprinted with permission from Lutz (1976).

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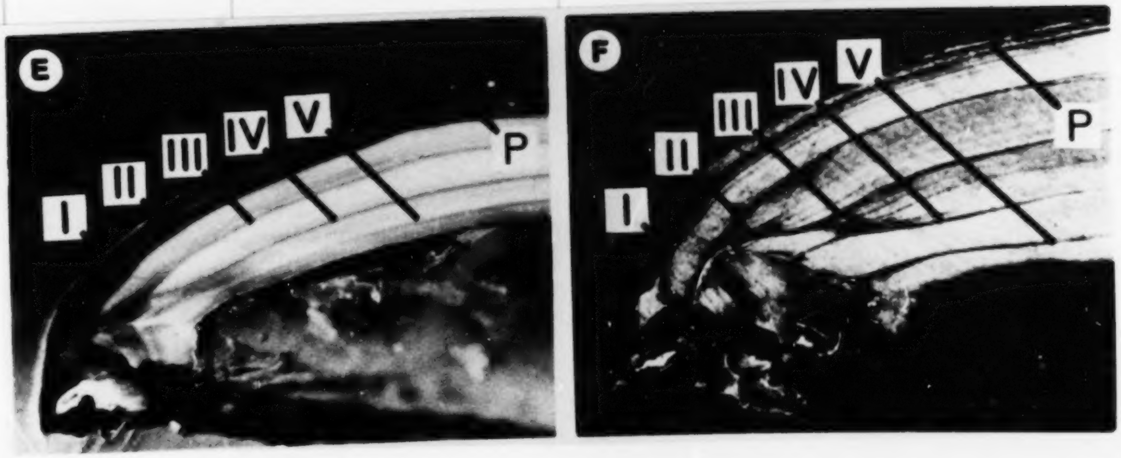

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Fig. 17 (e & f)

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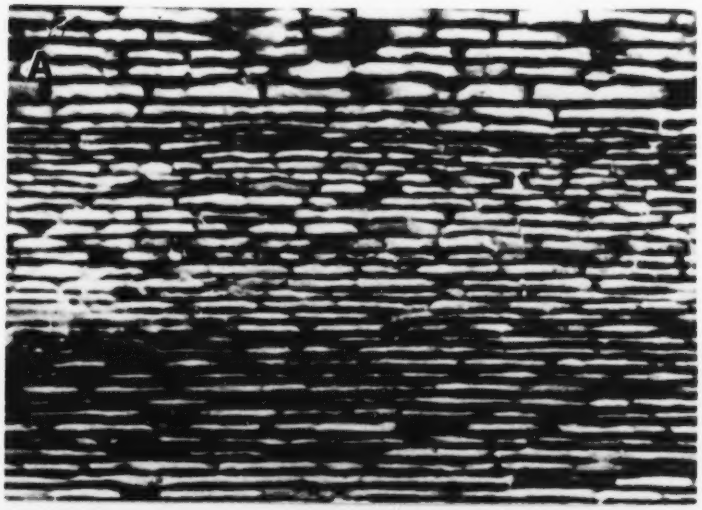

Fig. 18. (a) Scanning electron micrographs of polished and etched antero-posterior longitudinal sections of the inner nacreous shell layer of *Mytilus edulis* L. All specimens were sampled from the Damariscotta River, Lincoln County, Maine. (A) Annually formed ultrastructural crystalline pattern. The most recently formed aragonite crystalline laminae are at the bottom of the micrograph. x3400. (B) Aragonite crystalline laminae adjacent to the inner shell surface (gs) of a specimen sampled 18 June, 1974 x1700. (D) Aragonite crystalline laminae adjacent to the inner shell surface (gs) of a specimen sample 2 July, 1974. Although the actual junction between thick and thin laminae is above the upper border of the micrograph, a gradual increase in the thickness of crystal laminae with decreasing distance from the inner shell growth surface (gs) is apparent. x1700. Reprinted with permission from Lutz (1976).

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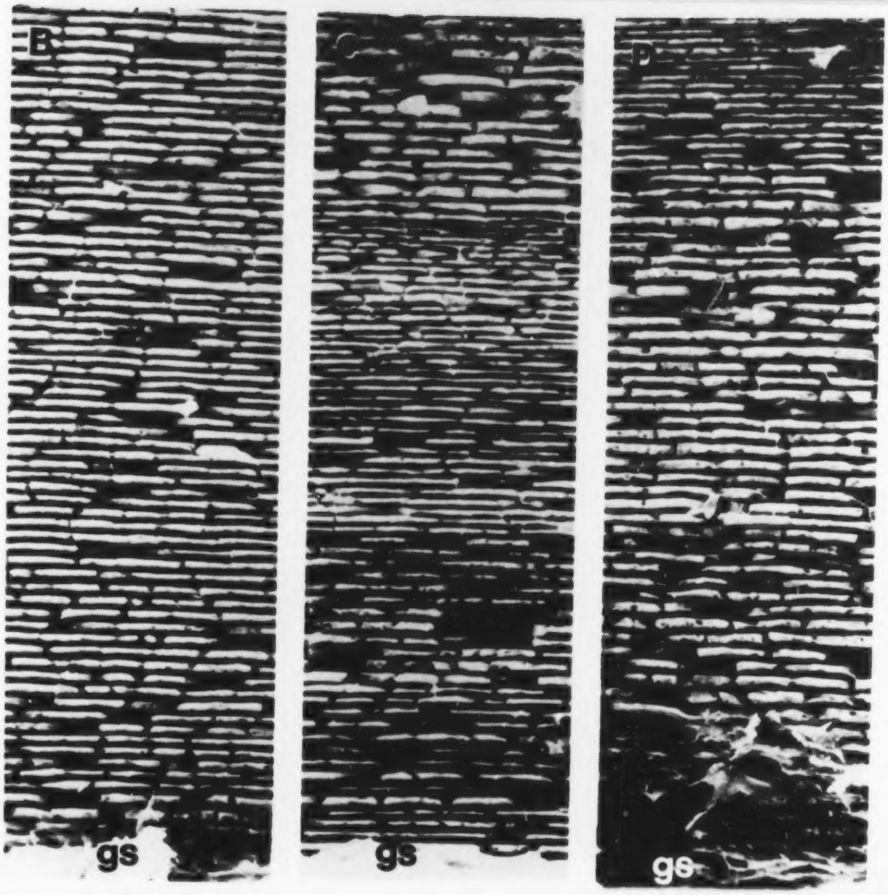

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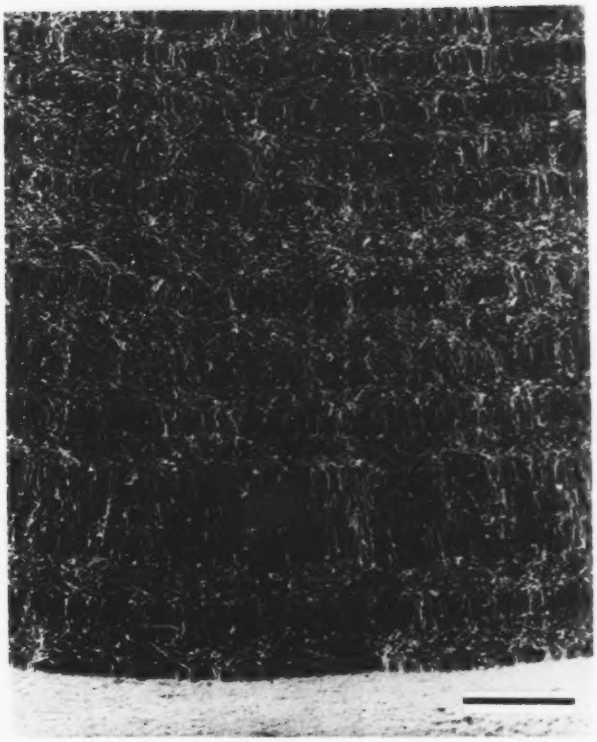

Fig. 19. Scanning electron micrograph of a vertical fracture through the inner shell layer of *Artica icelandira* near the umbo. Bands of simple aragonitic prisms are seen alternating with complex crossed-lamellar structures. Scale bar: 40 micrometers.

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CHAPTER 3

SHELL MICROGROWTH ANALYSIS: *MERCENARIA MERCENARIA* AS A TYPE EXAMPLE FOR RESEARCH IN POPULATION DYNAMICS

by

Michael J. Kennish

Environmental Scientist
Environmental Affairs Department
Jersey Central Power & Light Company
Madison Avenue at Punch Bowl Road
Morristown, New Jersey 07960

CHAPTER 3

I. INTRODUCTION

The molluscan shell has been the subject of intensive research in ecology and paleoecology for many years. Much of this research has centered around the examination of macroscopic growth features on the surfaces of shells of marine bivalves and the utilization of these growth bands in the investigation of environmental and paleoenvironmental problems in the marine ecosystem. Recent studies of microscopic growth features within the shells of various molluscan taxa, however, have revealed a more detailed and higher resolution record of growth. These internal shell microgrowth patterns in molluscs have proven to be valuable for reconstructing habitat conditions in both ancient and extant marine environments. Such patterns also yield information about population dynamics that are difficult or impossible to obtain by other methods.

A molluscan species ideally suited for shell microgrowth research is the coastal marine bivalve, *Mercenaria mercenaria* (Linné), which ranges from the Gulf of St. Lawrence to the Gulf of Mexico (Saila and Pratt 1973). This infaunal bivalve lies in the intertidal and shallow subtidal zones. During the past 15 years, the shell microstructure of *M. mercenaria* has been extensively studied (Barker 1964; Pannella and MacClintock 1968; Rhoads and Pannella 1970; Cunliffe 1974; Cunliffe and Kennish 1974; Kennish and Olsson 1975; Kennish 1976, 1977a, 1977b, 1978; Lutz and Rhoads 1977; Gordon and Carriker 1978). These workers have documented the remarkably well-preserved record of growth retained within the shell of this clam.

Because shell growth of *M. mercenaria* is strongly influenced by environmental conditions, shell microgrowth patterns effectively reflect conditions in the organism's ambient environment. External environmental factors affect a bivalve's physiology and hence its shell microgrowth patterns. Physiological events such as reproduction are also recorded. Analysis of the shell microstructure, therefore, can yield important data on the population dynamics of the species.

This chapter consists of a detailed description of patterns of growth increments and growth breaks in *M. mercenaria* and the environmental and physiological significance of each pattern. I will give a detailed example of how these microgrowth patterns can be used to approach an ecological problem: the investigation of the population dynamics of *M. mercenaria* in a lagoonal-type estuarine system. The objective of this chapter is to demonstrate how the ontogenetic shell growth record of *M. mercenaria* can serve as a "type" example for ecological and paleoecological research in other molluscan species.

II. SHELL MICROGROWTH PATTERNS IN *MERCENARIA MERCENARIA*

The shell of *M. mercenaria* is composed primarily of calcium carbonate (aragonite) and conchiolin. A vertical section through a valve reveals four shell layers: (1) the inner homogeneous layer; (2) the pallial myostracum (pallial muscle-scar layer); (3) the middle layer; and (4) the outer layer (Pannella and MacClintock 1968) (Fig. 1). Shell microgrowth patterns are most conspicuous in the outer layer, where shell growth reaches a maximum and growth increment widths exceed those in the inner and middle layers.

Three stages of growth (youth, maturity, and old age) are evident in valve cross-sections of this species (Cunliffe 1974). In youth, which persists for approximately 2 years, the outer shell layer terminates in concentric ridges at the outer shell surface, with growth increments intersecting the outer shell surface nearly at right angles. When the mature stage of growth is attained, the concentric ridges disappear and growth increments become recurved in shape. The beginning of the mature stage of growth corresponds closely with the onset of sexual maturity and lasts for 3-8 years. The final stage of growth is old age, and at this time crossed-lamellar shell structure completely replaces prismatic shell structure in the outer shell layer, growth increments become thin and perpendicular to the outer shell surface, and numerous growth breaks develop.

In order to study shell microgrowth patterns of *M. mercenaria* throughout the three ontogenetic stages outlined above, valves of specimens are sectioned perpendicular to the shell surface from the umbo to the ventral margin along the maximum axis of growth (see Chapter 1 for description of this axis; see also Appendix 1). Next, acetate peel replicas of the acid-etched cross-sections of the valves are made according to the method outlined in Appendix 1. Microgrowth patterns in the peels are studied microscopically. Shell microgrowth patterns can also be investigated in thin-sections of shell material, but thin-sections require considerably more preparation time and, therefore, place practical limits on sample size (see Appendix 1).

Using acetate peels and thin-sections, Pannella and MacClintock (1968), Rhoads and Pannella (1970), Cunliffe and Kennish (1974), Kennish and Olsson (1975), and Kennish (1978) analyzed shell microgrowth patterns of *M. mercenaria*. They recognized two categories of microgrowth patterns based on cyclical and interrupted growth incrementation. The first category, cyclical growth patterns, includes subdaily, daily, bidaily, fortnightly, lunar monthly, and annual types (Table 1). These result from variable rates of calcium carbonate deposition and/or dissolution (Lutz and Rhoads 1977; Gordon and Carriker 1978; see Chapter 2 for detailed discussion). Environmental conditions (Clark 1974) and a biological clock mechanism in the clam (MacClintock and Pannella 1969; Thompson and Barnwell 1970; Thompson 1975) appear to control the formation of such cyclical growth patterns. The second category, growth breaks, reflects periods of environmental and physiological stress. Seven types of growth breaks are documented, and they develop from both random and periodic events (Table 2). These consist of growth breaks caused by: freeze-shock (winter), heat-shock (summer), thermal-shock, shell margin abrasion, spawning, neap-tides, and storms.

Cyclical Growth Patterns

Cyclical growth patterns, viewed in cross-section, appear as an alternation of calcium carbonate-rich layers and organic-rich lines (Plate I a-c). Recent studies indicate that this repetitive sequence originates from alternating periods of shell secretion and dissolution during aerobic and anaerobic respiration, respectively (Lutz and Rhoads 1977; Gordon and Carriker 1978; see Chapter 2). When the valves of M. mercenaria are open and water is being pumped over the gills, the organism respires aerobically and the mantle deposits calcium carbonate and organic matrix simultaneously. During periods of shell closure, anaerobic metabolism occurs, and the concentration of succinic acid within the extrapallial fluid increases. Dissolution of shell calcium carbonate neutralizes the succinic acid produced during anaerobiosis, resulting in an increase in the concentration of calcium ions and succinate in the extrapallial and mantle fluids (Crenshaw and Neff 1969). This carbonate dissolution process leaves behind a conchiolin residue which forms organic-rich lines in the shell microstructure. With the return to aerobic conditions, shell decalcification ceases and a new phase of shell-building is initiated. Further details of this process are discussed in Chapter 2.

From a structural viewpoint, alternating periods of shell secretion and decalcification result in growth increments in the shell of M. mercenaria. Barker (1964), Pannella and MacClintock (1968), Rhoads and Pannella (1970), Cunliffe (1974), Cunliffe and Kennish (1974), Thompson (1975), Kennish and Olsson (1975), and Kennish (1976, 1977a, 1977b, 1978) have documented daily growth increments in the shell of this species indicative of a circadian rhythm (Plate I a-c).

The existence of a circadian rhythm in shell growth of M. mercenaria has been confirmed by mark and recapture experiments. For example, Rhoads and Pannella (1970) investigated shell microgrowth patterns of specimens that had been notched at the ventral margin of the shell, placed in sediment-filled plastic trays, and transplanted to intertidal and subtidal zones in Connecticut and Massachusetts. Individuals retrieved several months after transplantation were found to have faithfully recorded the transplant sequence on a daily basis. Similarly, Cunliffe (1974, personal communication) and Kennish (1977a, 1977b, 1978) transplanted several thousand notched clams to intertidal and subtidal zones in New Jersey. Specimens subsequently recovered and studied contained approximately the same number of growth increments in the outer shell layer as the number of days that had elapsed since the day of transplantation. When a daily growth increment was missing in the outer shell layer, it corresponded to a growth break in the shell. Pannella and MacClintock (1968) demonstrated the ability of M. mercenaria to add an increment of shell each day, even under strong adverse conditions. Clams kept in tanks for several months without any food deposited a thin growth increment every day. Other specimens placed on a table for seven days secreted seven thin growth increments.

A daily growth increment in *M. mercenaria* appears as a calcium carbonate-rich region between successive, well-developed organic-rich lines. The character of daily growth increments is strongly influenced by environmental conditions through physiologic responses of the bivalve (see Chapter 2). Water temperature, salinity, tides, water depth, substratum, storms, food supply, spawning events, and the individual's age affect the thickness of daily growth increments. Of these factors, water temperature and age appear to exert the major controlling influence on growth.

The rate of shell growth of *M. mercenaria* peaks between 20-25°C (Ansell 1968; Kennish and Olsson 1975) and decreases rapidly below 10°C and above 30°C. Growth rates reach maximum levels in clams between 1-3 years of age and minimum levels in clams greater than 5 years of age (Ansell 1968; Kennish 1977b). Studies by a number of workers show that seasonal growth rates are highest in the summer when water temperatures are elevated (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Cunliffe 1974; Kennish and Olsson 1975; Kennish 1978). Evidence of differences in the seasonal growth rates of *M. mercenaria* exists in the shell microstructure of specimens collected in Barnegat Bay, New Jersey, a temperate East Coast estuary with an annual water temperature range of -1.5 to 28.0°C. During the summer, these clams form thick daily growth increments ranging from 15-150 μm (Plate I a-c), whereas during the winter, they form thin daily growth increments ranging from 1-50 μm (Plate I d-f). Daily growth increments in the spring and fall are intermediate in thickness between summer and winter increments and range from 10-75 μm in thickness.

Occasionally, daily growth increments are grouped into a bidaily microgrowth pattern. Although formed in the shell of *M. mercenaria* during most seasons of the year, the bidaily pattern is not as common as subdaily, daily, fortnightly, and annual types. Bidaily patterns consist of an alternating sequence of one thick and one thin growth increment formed during a 48-hour period (Plate I g). The cause of these couplets is unknown.

A subdaily microgrowth pattern consists of one or more diffuse organic-rich lines within a daily growth increment (Plate I h). Subdaily lines represent organic (conchiolin) residues left behind as a result of shell dissolution during periods of shell closure and anaerobiosis (Gordon and Carriker 1978; see also Chapter 2 for discussion). Data from Gordon and Carriker (1978) indicate a causal relationship between rhythms of valve movement in the clam and the appearance of the diffuse organic-rich lines. The rhythms of valve movement range from 5.4 to 12.8 hours in different individuals.

The subdaily pattern is commonly encountered in intertidal clams but also has been found in subtidal specimens. Kennish and Olsson (1975) attributed the formation of subdaily lines in some specimens to semidiurnal low tides. This suggests that such a pattern is associated with valve closure during low tide.

In addition to semidiurnal events, the shell of *M. mercenaria* contains a record of spring and neap tides, as well as the lunar months. Spring and neap tide events appear as a clustering of daily growth increments into a fortnightly pattern composed of six to eight thick increments followed by six to eight thin increments (Plate I i). The series of thick increments are formed during spring tides and the series of thin increments during neap tides. Although the fortnightly microgrowth pattern occurs in the shell of nearly all specimens of this species, it is, like the subdaily pattern, more conspicuous in individuals from the intertidal zone which are most strongly influenced by the tides.

Groupings of pairs of tidal clusters, with an overall periodicity of 29 days, comprise the lunar month microgrowth pattern (Plate I j). This pattern has a periodicity equivalent to that of the synodic month, and it is manifested on the external shell surface by concentric ridges formed by the thickened outer shell layer. The lunar month microgrowth pattern occurs infrequently in M. mercenaria.

Annual periodicities in water temperature, food supply, light input, and perhaps other environmental variables result in annual cycles in the thickness of growth increments. This annual periodicity is strongly developed in M. mercenaria. Low water temperature and a reduced food supply in the winter result in slow shell growth (thin daily growth increments), whereas high water temperature and an abundant food supply in the summer accelerate growth (thick daily growth increments). Freeze and heat-shock breaks are also commonly associated with seasonal periodicities.

Growth Breaks

Research on transplanted and natural populations of M. mercenaria indicate that extremes in environmental conditions, rapid changes in environmental conditions, and other physiological stresses can preclude shell secretion for a period of 24 hours or more. During such a period, the valves of the organism remain closed, anaerobic respiratory pathways are employed, and shell decalcification takes place (Crenshaw and Neff 1969; Lutz and Rhoads 1977; Gordon and Carriker 1978; see Chapter 2). Some clams withdraw their mantle when stressed, producing V-shaped notches in the outer shell layer (Plate II a-c). These notches have been termed "growth breaks" (Cunliffe 1974; Kennish and Olsson 1975; Kennish 1977a, 1977b, 1978).

Some growth breaks are extensive, leaving U-shaped notches in the outer shell layer that can be observed on the external shell surface as concentric "growth" lines, linear depressions, or rings. When viewed in shell cross-section, crossed-lamellar shell structure and an increased concentration of shell organic material are usually associated with the region of the breaks. These microstructural changes may enable the bivalve to strengthen its shell during periods of severe environmental or physiological stress (MacClintock 1967). Other kinds of depositional breaks are difficult to distinguish on the exterior of the shell because they represent only a few micrometers of change in the microstructure. These are generally not associated with crossed-lamellar shell structure or a high organic content.

It is nearly impossible to identify the diverse origins of growth breaks by examining only the exterior of the shell. By studying the shell microstructure, however, the origin of many growth breaks can be established. Each type of growth break can be identified in the microstructure because each one is preceded and followed by a unique pattern of daily growth increments and shell structural changes.

Of the seven types of growth breaks known to occur in *M. mercenaria*, four are associated with periodic events (freeze-shock, heat-shock, spawning, and neap tides) and three with semi-periodic or random events (thermal-shock, abrasion, and storms). Shock-breaks are particularly abundant and noticeable in the shell of this species; they are caused by temperature stress. For example, freeze- and heat-shock breaks, although developed during different seasons of the year, have similar characteristics. Both occur after a gradual decrease in overall shell convexity and consist of very thin increments prior to and following the break. Also, a pronounced U- or V-shaped notch is developed in the outer shell layer bordered by a region of high organic content; crossed-lamellar shell structure transgresses and replaces prismatic shell structure on one, or each, side of the break (Plate II a-c).

The thin increments preceding a freeze-shock break represent a decline in shell deposition in the fall and winter as water temperature drops below the optimum for growth in the species. The depositional break generally arises at the time of the first freeze of the year but may also take place later in the winter season. The gradual increase in the thickness of growth increments subsequent to the break is indicative of physiological recovery from the period of temperature stress.

In contrast to a freeze-shock break, thin growth increments preceding a heat-shock break result from the gradual rise in water temperature above the optimum for growth in the species. The depositional break occurs during the period of maximum summer temperatures. The increase in the thickness of growth increments after the break, similar to that of a freeze-shock break, represents physiological recovery from the temperature stress.

Freeze- and heat-shock breaks do not develop at exactly the same time each year because seasonal water temperatures vary from one year to the next. Within a given population, however, these breaks occur synchronously in a large number of individuals. This synchronous effect allows the determination of age, growth rate, and mortality patterns of the population.

Rapid short-term changes in water temperature, can also create breaks in accretionary shell growth of *M. mercenaria*. Kennish and Olsson (1975) and Kennish (1976) have shown that shells of clams at the mouth of Oyster Creek in Barnegat Bay, New Jersey, contain thermal-shock breaks due to sudden fluctuations in water temperature (up to 5°C) associated with thermal discharges from the Oyster Creek Nuclear Generating Station. Thermal-shock breaks form specifically when the station undergoes abrupt shutdowns, massive load reductions, and rapid renewal of operations following shutdown or load reduction periods.

A thermal-shock break appears as a V-shaped notch in the outer shell layer which is accompanied by crossed-lamellar shell structure extending from the middle shell layer into the outer shell layer. Thin increments of growth follow the break. The thermal-shock break can be distinguished from freeze- or heat-shock breaks by its sudden occurrence, the lack of growth deceleration prior to the break, the massive slow down in growth following the break, and its formation during all seasons of the year (Plate II e-g).

By counting daily growth increments backward from the valve margins of freshly killed specimens, it is possible to accurately date the time of formation of thermal-shock breaks. These events are represented in most individuals of a population and, therefore, serve as useful reference marks in the correlation of other ecological stresses that take place during the life span of the population. Thus, thermal-shock breaks are of value in the study of the population dynamics of clams subjected to thermal discharges.

Random anthropogenic effects, other than thermal discharges, may also produce growth breaks in *M. mercenaria*. For example, the abrasion of shells of specimens during transplantation experiments often interrupts shell deposition sufficiently to cause a disturbance band (Pannella and MacClintock 1968; Rhoads and Pannella 1970; Kennish 1978). Shell abrasion results in a growth break similar in morphology to the thermal-shock break, with a sequence of thin increments of growth following a V-shaped notch (Plate II h-i).

The shell of *M. mercenaria* also preserves a record of biological events; for example, spawning periods. Depending on geographical location, spawning in the species ranges from late spring to early fall as water temperature increases above 20°C (Ansell 1968). Carriker (1961) noted maximum frequency of spawning in clams in Little Egg Harbor, New Jersey, between 24-26°C. Spawning is synchronous, stimulated in part by water temperature and by a hormone carried in the sperm (Nelson and Haskin 1949).

At the time of spawning, the bivalve suddenly stops feeding, and its growth slows down substantially. This sequence is expressed in the shell as an abrupt break in growth preceded by little or no reduction in the thickness of growth increments and is followed by a series of thin growth increments which reflects reproductive stress (Plate II j). Recovery from the stress is rapid; the thickness of growth increments quickly returns to the thickness observed prior to spawning. Breaks caused by spawning are less severe than freeze-, heat-, and thermal-shock breaks, with notches in the shell being thinner and shallower in the outer shell layer. Crossed-lamellar shell structure may, or may not, be associated with reproductive breaks.

Spawning breaks in *M. mercenaria* do not develop until the bivalve attains sexual maturity at an age of 2 years (Rhoads and Pannella 1970). Some individuals have more than one reproductive break per year, and males display more spawning breaks than females (Pannella and MacClintock 1968). Thus, within the same population, males should be smaller than females of the same age.

Cunliffe (1974) described clams which had spawning breaks coincident with neap tides. His work supported an earlier observation by Carriker (1961) that showed mass spawning of *M. mercenaria* during neap tides. Spawning at this time in the fortnightly tidal cycle serves to retain larvae in the estuary because there is less exchange of water with the open ocean during neap tides than during spring tides.

Extreme neap tides may cause a growth break at times other than spawning, especially in intertidal and tide pool clams. The neap-tide break is preceded by a group of increments decreasing in thickness toward the break and followed by a series of increments increasing in thickness away from the break. Notches in the outer shell layer generally are less deeply incised than those associated with other types of breaks, and crossed-lamellar shell structure is usually not associated with the region of the break.

Another type of growth break identified in the shell of this species is the storm break. The features of the storm break vary, depending on the severity of the storm and the depth of the clam below sea level. In most cases, the thickness of growth increments during pre- and post-storm periods is about the same. The break appears suddenly and it may contain silt grains trapped deep within an indentation in the prismatic shell layer (Plate II k). The silt grains become trapped between the mantle and shell during the storm and are incorporated in the microstructure when growth resumes after the storm.

Other types of breaks, some of anthropogenic origin, could occur in the shell microstructure of *M. mercenaria* but have not yet been documented. Floods, sedimentation events, attacks by predators, disease, and changes in water chemistry may also produce structural changes in the shell. Variations in turbidity and substrate stability associated with dredging operations also are capable of affecting shell secretion. Additional experimentation on this species should continue, therefore, to determine the causal relationship between specific anthropogenic, environmental, and physiological events and microgrowth patterns.

III. APPLICATION TO ANALYSIS OF POPULATION DYNAMICS

Microgrowth patterns in the shell of *M. mercenaria* accurately record environmental and physiological conditions throughout the ontogeny of the organism, enabling applications to various ecological and paleoecological problems. A number of applications of this type have been made in the past. For example, Barker (1964) investigated changes in the thickness of growth increments with respect to latitude in extant *M. mercenaria*, as did Cunliffe (1974). Cunliffe (1974) also described the paleoecology of the Choptank and St. Mary's Formations (Middle Miocene age) in Maryland by examining growth increments in fossil *M. mercenaria*. Rhoads and Pannella (1970) studied the influence of substratum, water depth, turbidity, and temperature on juvenile *M. mercenaria* by analyzing the shell microstructure in transplanted specimens. Kennish and Olsson (1975) and Kennish (1976, 1977a) evaluated the impact of thermal discharges from the Oyster Creek Nuclear Generating Station on shell microgrowth patterns of clams in Barnegat Bay, New Jersey.

Although a substantial volume of data on shell microgrowth patterns has been gathered on the behavior of this bivalve, there has been no attempt to determine its population dynamics by utilizing shell microstructure. In general, research on the population dynamics of an organism requires the analysis of size-frequency histograms of a population. This usually demands a great deal of time and effort on the part of the investigator (see Chapter 5). By implementing shell microgrowth analysis, however, these problems can be mitigated or eliminated because of the life history data stored within the shell of each clam.

Studies of population dynamics include defining the age and growth rates of organisms and their mortality and recruitment patterns (Hallam 1972). In the case of *M. mercenaria*, these data are obtainable by microstructural analysis of the shell, if the daily growth increment is used as the fundamental unit of study. For instance, counts of daily growth increments from the umbo to the ventral valve margin yield data on the absolute age of the animal. If the thicknesses of daily growth increments are measured, daily and yearly growth rates and size distributions can be established. Superimposing growth rates on the size distributions of life assemblages of clams supplies information on the frequency and success of recruitment (Kennish 1978).

By adapting these methods of analysis to dead specimens, it is possible to determine the absolute age at death, as well as the growth rates of specimens of death assemblages (Rhoads and Pannella 1970). These data can be used to generate life tables which accurately depict mortality of a population. In addition to providing data on the absolute age at death, growth increment counting in combination with the interpretation of microgrowth patterns at the valve margin can yield season of death data (Rhoads and Pannella 1970; Tevesz 1972). For example, a ventral margin following a complete sequence of winter growth increments and growth breaks implies spring death (Plate III a-c). A heat-shock break (Plate III e), a spawn break (Plate III f-g), and a summer storm break (Plate III h) adjacent to the growing edge of the shell signify summer death, as do thick growth increments at the outer edge preceded by a freeze-shock break located 160-200 increments dorsally (Plate III i-j). A ventral margin preceded by a long period of summer growth increments and growth breaks suggests fall death (Plate IV a-d). Thin growth increments located at the shell edge approximately 160-200 increments ventrally from a heat-shock break denote winter death (Plate IV e). A freeze-shock break found at the ventral margin also connotes winter death (Plate IV f-h).

Analysis of microgrowth patterns at the valve margin can be of value in differentiating between types of mortality in *M. mercenaria* populations (i.e. natural *vs* census or catastrophic mortality). A population experiencing natural mortality will consist of individuals with a high degree of variability in the terminal microgrowth patterns of their shells, indicating the organisms died during different seasons of the year. Census (mass) mortality, in contrast, will be manifested by great similarity in the terminal microgrowth patterns of component shells of a death assemblage, reflecting widespread mortality during a single season of the year.

It is feasible to use shell microgrowth patterns to define different generations of clams within a death assemblage. Some growth breaks (i.e. freeze-shock and heat-shock breaks) occur synchronously in a large part of a population whereas other (i.e. thermal-shock and storm breaks) can be dated precisely by alternate methods (Kennish 1978). In effect, it is often possible to match and date these growth breaks across many individuals in a death assemblage, employing each break as a microgrowth datum for purposes of correlation. Those specimens with a significant correlation in their growth breaks have a high probability of belonging to the same generation of clams.

IV. POPULATION DYNAMICS OF *MERCENARIA MERCENARIA* IN BARNEGAT BAY, NEW JERSEY

In a previous study, I examined size and age distributions, growth rates, and recruitment and mortality patterns of *M. mercenaria* by implementing the methods of shell microgrowth analysis described above (Kennish 1978). This work was conducted in Barnegat Bay, New Jersey, a shallow tidal basin located midway on the eastern New Jersey coast (Fig. 2). Results of this study are summarized below.

Size and Age Distributions, Growth Rates, and Recruitment Patterns

I sampled death assemblages of *M. mercenaria* at 4 sites in Barnegat Bay (sites 1, 3, 4 and 7, Fig. 2) in the summer of 1974 and collected life and death assemblages of the bivalve from 9 sites in the summer of 1976 (sites 1-9, Fig. 2) (Kennish 1978). Size measurements on individuals were made from the umbo to the ventral valve margin at a slight angle to the dorso-ventral plane for the purpose of investigating the entire growth record of the clam (Plate IV i). The axis measured only approximates the height of the organism; therefore, it was labeled h' to differentiate it from true shell height (h).

Figures 3 and 4 illustrate the size distributions of all *M. mercenaria* collected in the summers of 1974 and 1976, and Table 3 summarizes these distributions. The size-frequency distributions of all death assemblages and most of the life assemblages consist of unimodal curves with negative skewness. These indicate a great similarity in clam sizes throughout the estuary except at Barnegat Inlet (site 5) where juveniles comprise both the life and death assemblages. Barnegat Inlet, however, is a transitional environment between the Atlantic Ocean and Barnegat Bay, and environmental conditions in the inlet are quite different from those within the estuary. These differences may account for spatial variations in recruitment and growth of the species in the area of study.

Research on extant and fossil invertebrate assemblages has shown that growth rates, recruitment, and mortality primarily control the form of size-frequency distributions of invertebrate populations (Craig and Hallam 1963; Craig and Oertel 1966; Craig 1967; McKerrow et al. 1969; Schmidt and Warme 1969; Levinton and Bambach 1970; Hallam 1972; see also Chapter 5). The two major factors influencing the shape of size-frequency distributions of death assemblages are growth rates and mortality (Hallam 1972). Evidence of seasonal recruitment rarely exists in death assemblages because annual fluctuations in recruitment tend to average out through the accumulation of many generations of clams; this contributes to the formation of unimodal size-frequency distributions. Recruitment patterns are preserved best in mass mortality assemblages where the size-age distribution of the life assemblage is "frozen" at a time surface (Sheldon 1965).

To test these principles on *M. mercenaria* in Barnegat Bay, I sectioned and analyzed the valves of 277 specimens from death assemblages gathered in 1974 at sites 1, 3, 4, and 7 (Kennish 1978). The valves ranged from 14.0 - 76.5 mm in h'. Daily growth increment and seasonal growth break counts were made on the valves to obtain absolute growth rates of the specimens.

Tables 4 and 5 show the mean and absolute age-h' relationships of the clams at each site, and Table 6 gives the pooled age-h' values of the 277 individuals. Most of the clams are less than 7 years of age and 70.0 mm in h'. Growth rates of the specimens are uniform at all four sites, with growth being more rapid during youth than maturity and old age. The bivalve undergoes a gradual, exponential decline of growth rate with increasing age; growth is nearly linear during the juvenile stage.

This type of ontogenetic growth conforms best to the following exponential growth equation:

$$\text{(differential form)} \quad dN/dt = N_{max}r_o - r_oN_t$$

$$\text{(integrated form)} \quad Nt = N_{max}\ (1 - ce^{-r_ot})$$

where dN/dt is the rate of shell growth, N_{max} the asymptotic h' or maximum h' attainable, r_o the maximum intrinsic rate of natural increase, N_t the h' at a given time t, c the integration constant defining the complement of that proportion of N_{max} which specifies the initial N_o, and e the base of the natural logarithm (Kennish 1977b). This exponential growth equation predicts growth curves for M. mercenaria that are realistic in comparison to other exponential functions.

A comparison of the observed growth rates of specimens within death assemblages of clams at sites 1, 3, 4, and 7 (Table 5) with the corresponding size-frequency distributions at these locations (Figs. 3a-3d) indicate that most specimens in these samples range from 40-70 mm in h' corresponding to ages of 4-9 years. Mortality is highest in larger and older clams, and this reflects the effect of high rates of death during theierontic stage of life. Thus, the unimodal, size-frequency distributions of negative skewness in the death assemblages result from an interplay of growth rates that decrease with age and mortality that increases with age. The similar size distributions of the death assemblages suggest comparable growth and mortality patterns throughout the estuary.

Most M. mercenaria in the life assemblages, as in the death assemblages, range from 40 to 70 mm in h'. Most live clams in Barnegat Bay, therefore, are in old age. The unimodal, negative skewness of the life assemblage distributions reveals a recent failure of annual recruitment in the bay.

Mass spawning and recruitment of M. mercenaria occurs in the summer in New Jersey. If recruitment had been successful in the early and mid 1970's, modes corresponding to successive yearly broods should be found in the size-frequency distributions of the life assemblages. A theoretical model simulating these conditions is depicted in Figure 5. This model delineates a polymodal size-frequency distribution of an ideal, stable clam population that experiences constant annual recruitment and no mortality. Modes in the model at 1.5 mm, 10.9 mm, 22.2 mm, 33.0 mm, and 42.4 mm correlate with the 1976, 1975, 1974, 1973, and 1972 year classes, respectively, and are derived from the average rate of growth per year for M. mercenaria in Barnegat Bay (Table 6). Troughs between modes represent periods of growth of each generation from one recruitment stage to the next. Beyond 50 mm, the modes merge and the age classes become obscured because of the spread of sizes of older clams and the reduction in growth rates which causes an overlapping of the larger classes. This overlapping effect is also apparent in the observed size-frequency distributions of the life assemblages (Fig. 4).

A comparison of the observed size-frequency distributions of the life assemblages in Barnegat Bay with the size-frequency distributions of the model reflect the conspicuous absence of single year classes of clams in the estuary from 1973 to 1976. A sharp peak at 11.8 mm in the life assemblage distribution for site 5 (Barnegat Inlet) corresponds to the 1975 year class, and it relates well to the population growth model. The absence of modes at smaller and larger sizes, however, is a consequence of poor recruitment at this site prior to, and following, 1975.

Young *M. mercenaria* are being added to populations in Barnegat Bay not on an annual basis but sporadically. This recruitment pattern appears to be caused by the normal population dynamics of the species (Kennish 1978). Recruitment may fail for as long as five or ten continuous years, but a population can be successfully maintained by a single year of good recruitment.

Mortality Patterns

Absolute mortality patterns in death assemblages of *M. mercenaria* at sites 1, 3, 4, and 7 were resolved by shell microgrowth analysis. Data on the season of death, as well as on the size and age of the individual at the time of death permitted the construction of size- and age-frequency distributions, death-frequency histograms, and life tables for each death assemblage. This information was used to specify seasons of peak stress in the species and to determine the relationship between the size and age of the clam and mortality in the population. In addition, the information was utilized to reveal the effect of geographical location within the estuary on mortality of the organisms.

Table 7 shows the frequency of death of *M. mercenaria* per season based on the analysis of 278 valves of specimens sampled at the four sites in 1974. Mortality reaches a maximum in the summer and winter and a minimum in the spring and fall. Figure 6 displays this trend and indicates that seasonal mortality is similar at all sites.

I attributed the high summer mortality to the physiological stress of spawning and to increased predator and parasitic activity during the warmer months of the year (Kennish 1978). High winter mortality, however, I ascribed to physiological stresses related to harsh environmental conditions. During the winter, the bivalve lives on stored carbohydrate reserves because of low food supply and low water temperatures in the bay. However, these reserves may be inadequate in some individuals, especially during severe winters.

Absolute mortality of *M. mercenaria*, like seasonal mortality, is similar at sites 1, 3, 4, and 7. Evidence for this exists in the life tables constructed for the death assemblages at each location (Tables 8-11) which were formulated by using the methods of Deevey (1947), Barclay (1958), Reyment (1971), and Gani (1973). Larval mortality of *M. mercenaria* was not investigated; therefore, the life tables were constructed beginning at age one of a hypothetical cohort (radix) of 1000 clams.

All of the life tables show low mortality for clams between the age of 1 and 4 years. After the fourth year of life, mortality increases markedly, although less consistently, through the remaining age intervals. This pattern of mortality is graphically demonstrated by mortality curves drawn for the 4 assemblages (Fig. 7).

Mercenaria mercenaria larval mortality is known to be high (Thorson 1950; Carriker 1961); consequently, a survivorship curve projected for the entire ontogeny of this bivalve should be sigmoidal. A high probability of death exists for the meroplanktic stages because of disease, starvation, and predation, but the probability drops substantially after the organism settles onto a favorable substratum. The probability of death increases again in old age.

Based on the life table data, the risk of death of *M. mercenaria* begins to increase subsequent to the attainment of sexual maturity. To test this effect, I transplanted 1,486 clams to the substratum at sites 1 and 3, and recorded the mortality patterns of the experimental populations one year after transplantation (Kennish 1978). Each site received 743 specimens of comparable size (Table 12).

The valves of the clams were sanded at the ventral margin prior to transplantation to produce reference notches for shell microgrowth analysis. The experimental populations were transplanted in June 1975 and retrieved in June 1976. Empty valves of dead specimens were studied microscopically to determine their absolute age and season of death.

A total of 1000 live and dead clams were recovered at the two experimental sites in June 1976, representing 67% of the specimens originally transplanted. Table 13 compares the size (h')-frequency distributions of these clams. Most of the dead *M. mercenaria* were larger than 50 mm in h' (Fig. 8) and greater than 5 years of age (Fig. 9); thus, they were reproductively mature at the time of death.

These distributions conform well to those of the death assemblages of natural populations, although the frequency of death in the smaller and younger classes is greater in the experimental populations. The differences in absolute mortality between the natural and experimental populations are not substantial, considering that mortality in the natural populations constitutes a cumulative effect over many years, whereas mortality in the experimental population depicts only a single year effect. The death assemblages of the natural populations give a more realistic picture of mortality trends for *M. mercenaria*.

As in the death assemblages of natural populations, the seasonal frequency of death of the experimental populations peaks in the summer (Fig. 10). The low frequency of winter death in the experimental populations, however, stands in contrast to the high frequency of winter death in the natural populations (Fig. 6). This indicates the absence of a significant environmental stress on the experimental populations during the winter of 1975-76.

A number of inferences can be made on the population dynamics of *M. mercenaria* based on the size, age, and season of death data on the natural and experimental populations in Barnegat Bay. High mortality during both the larval and gerontic stages suggests that the bivalve is most susceptible to physiological and environmental stresses at these times. The life expectancy of the clam increases markedly after it successfully settles in an area and passes through the plantigrade stage ($\sim$ 10 mm in size). When the bivalve reaches sexual maturity at the age of 2 years, the probability of death is relatively low which ensures the survival of the species. Because mortality is relatively low between the plantigrade and gerontic stages, a young population can persist reasonably intact for several years at a time without the need of large-scale recruitment.

The gerontic stage is a period of diminished metabolism (Hopkins 1930), slowed growth, and increased mortality. High mortality at this time appears to be associated with physiological degeneration combined with environmental influences, although it is impossible to determine the relative contribution of either of these factors to observed mortality patterns by utilizing shell microgrowth analysis alone. Histological examination of soft parts in combination with the analysis of the shell microstructure may yield additional detailed information on the causes of mortality in many populations.

CONCLUSIONS AND FUTURE RESEARCH EFFORTS

Rhoads and Pannella (1970) discussed potential applications of molluscan shell microgrowth patterns in ecology and paleoecology. Many of these applications were formulated from observations on extant *M. mercenaria*. Since 1970, applications of shell microgrowth patterns to fossil *M. mercenaria* have lagged behind investigations on live specimens, but significant interdisciplinary advances in recent years have enabled applications to a number of paleoecological problems.

Perhaps the most useful application of shell microgrowth patterns in *M. mercenaria* is in the study of the population dynamics of the organism. For example, data on the season of death, age and size at the time of death, and absolute rate of growth of Recent populations of clams from various estuarine environments should be valuable to resource management programs assessing this commercially important bivalve. Determining the season of peak environmental stress would be important to aquaculture and future stock rebuilding programs.

Research on shell microgrowth patterns of live *M. mercenaria* in stressed environments may provide critical information on the biological consequences of man's activities on this species. For instance, data on shell microgrowth patterns of clams subjected to dredging and filling operations, domestic and industrial sewages, and oil spillages can reveal information of predictive value concerning population changes. By employing shells of death assemblages of *M. mercenaria* in these stressed environments, temporal and spatial changes of the populations can be related to anthropogenic factors.

Similar applications may be extended to other molluscan taxa. It is necessary, however, to establish the relationship of shell microgrowth patterns in these taxa to specific environmental parameters and physiological conditions. This requires a detailed analysis of live specimens from natural and experimental populations.

Once the analysis of shell microgrowth patterns in many extant molluscan taxa is accomplished, applications to fossil molluscan populations should proceed more rapidly. In the future, for example, it is conceivable that the analysis of microgrowth patterns in fossil molluscan populations from stratigraphic sequences of coastal plain formations along the Atlantic and Gulf coasts could be used to reconstruct paleolatitudes, paleoclimates, and paleobathymetry through the Tertiary period. It might also prove important in evolutionary studies of molluscs during this period of time.

Molluscan shell microgrowth patterns remain a viable tool for government, industry, and academic research. With continued interdisciplinary investigations into molluscan physiology, biochemistry, and shell structure, additional applications of the molluscan shell should be forthcoming. These applications should prove to be particularly helpful in the analysis of environmental and paleoenvironmental problems.

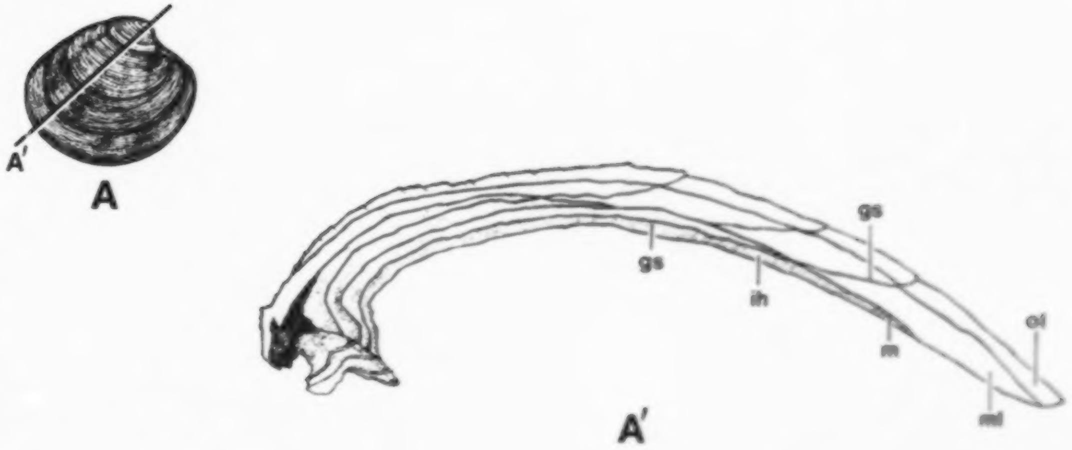


Fig. 1. Valve of Mercenaria mercenaria (Linné). A, outer surface view; approximately x0.5. A', valve cross-section showing growth surfaces (gs) and the four shell layers; inner homogeneous (ih), pallial myostracum (m), middle (ml), and outer (ol); approximately x2. (after Pannella and MacClintock 1968)

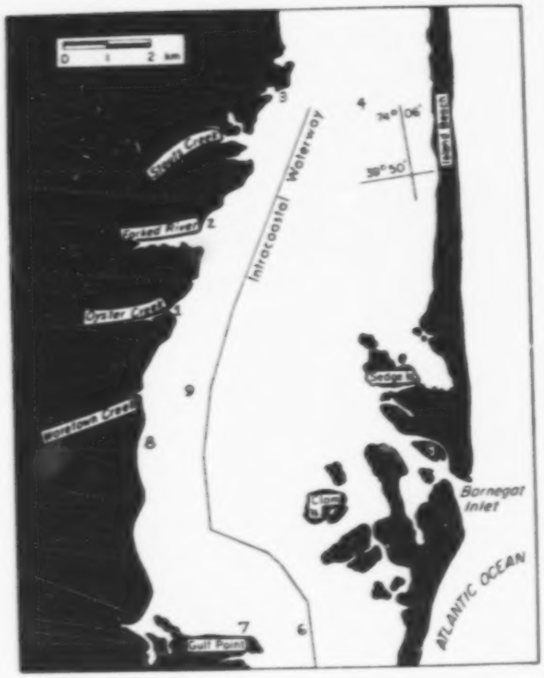
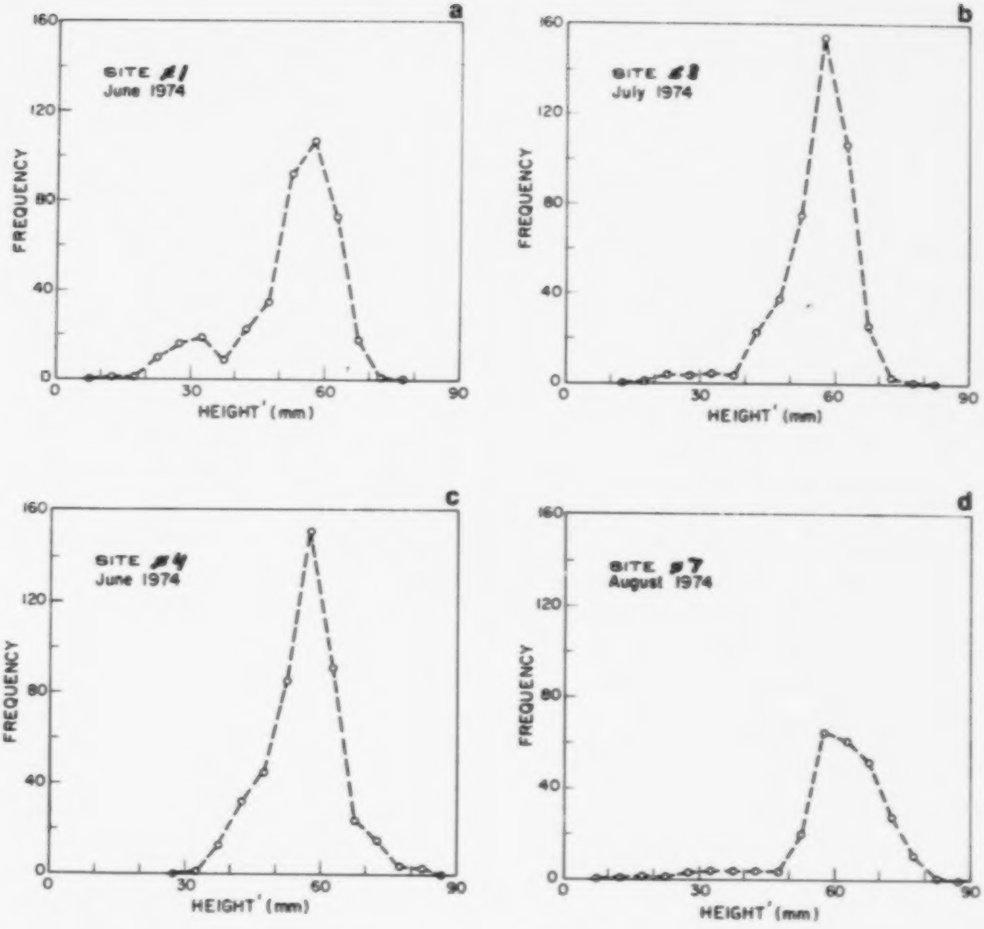
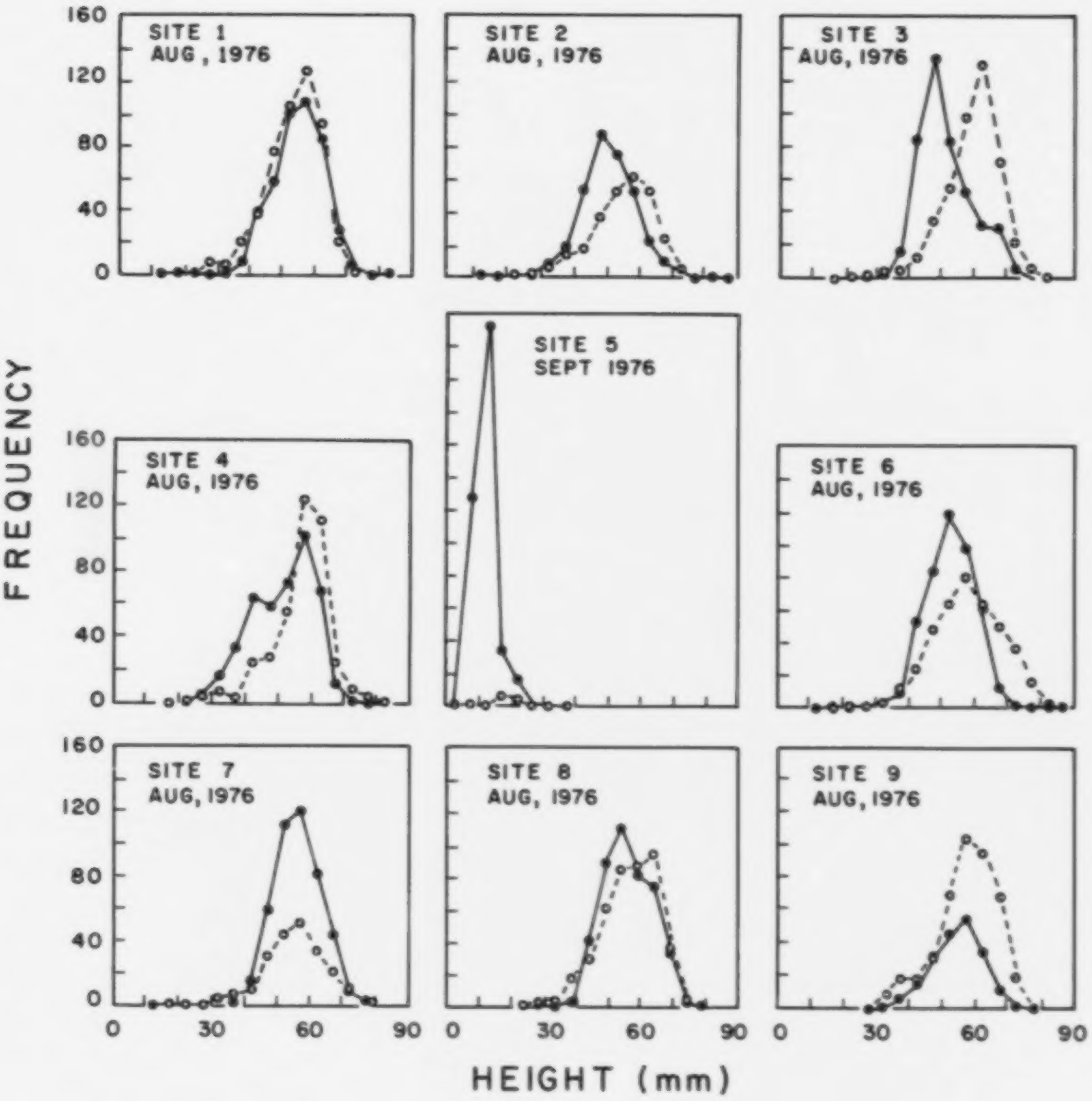


Fig. 2. Sampling locations of *Mercenaria mercenaria* in Barnegat Bay, New Jersey.



Figs. 3(a-d). Size (h')-frequency distributions for death assemblages of Mercenaria mercenaria collected at sites 1, 3, 4, and 7 in Barnegat Bay in 1974. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV i.



Figs. 4(a-i). Size (h')-frequency distributions for life and death assemblages of *Mercenaria mercenaria* collected at sites 1-9 in Barnegat Bay in 1976. (----) Death assemblages; (——) life assemblages. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV i.

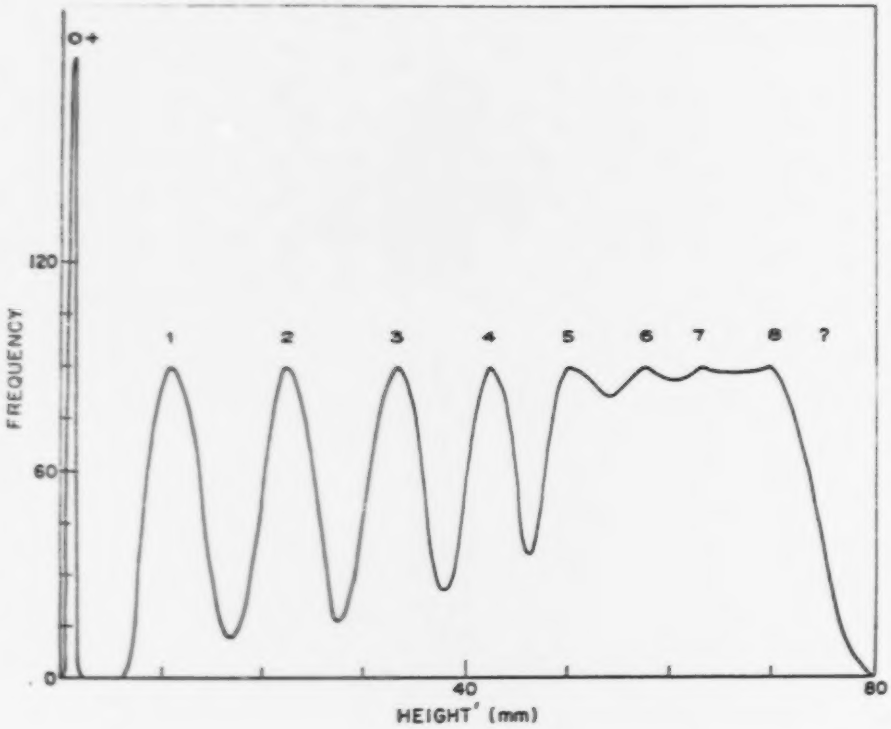


Fig. 5. Theoretical population model for eight years of growth of Mercenaria mercenaria in Barnegat Bay. The model assumes population stability with constant annual recruitment and zero mortality. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV i.

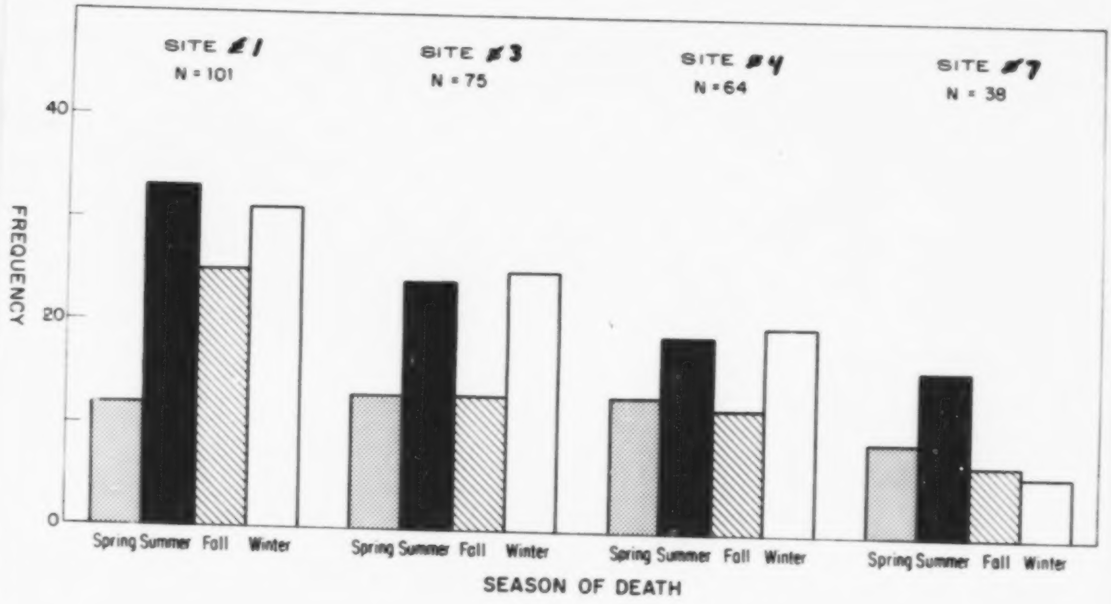
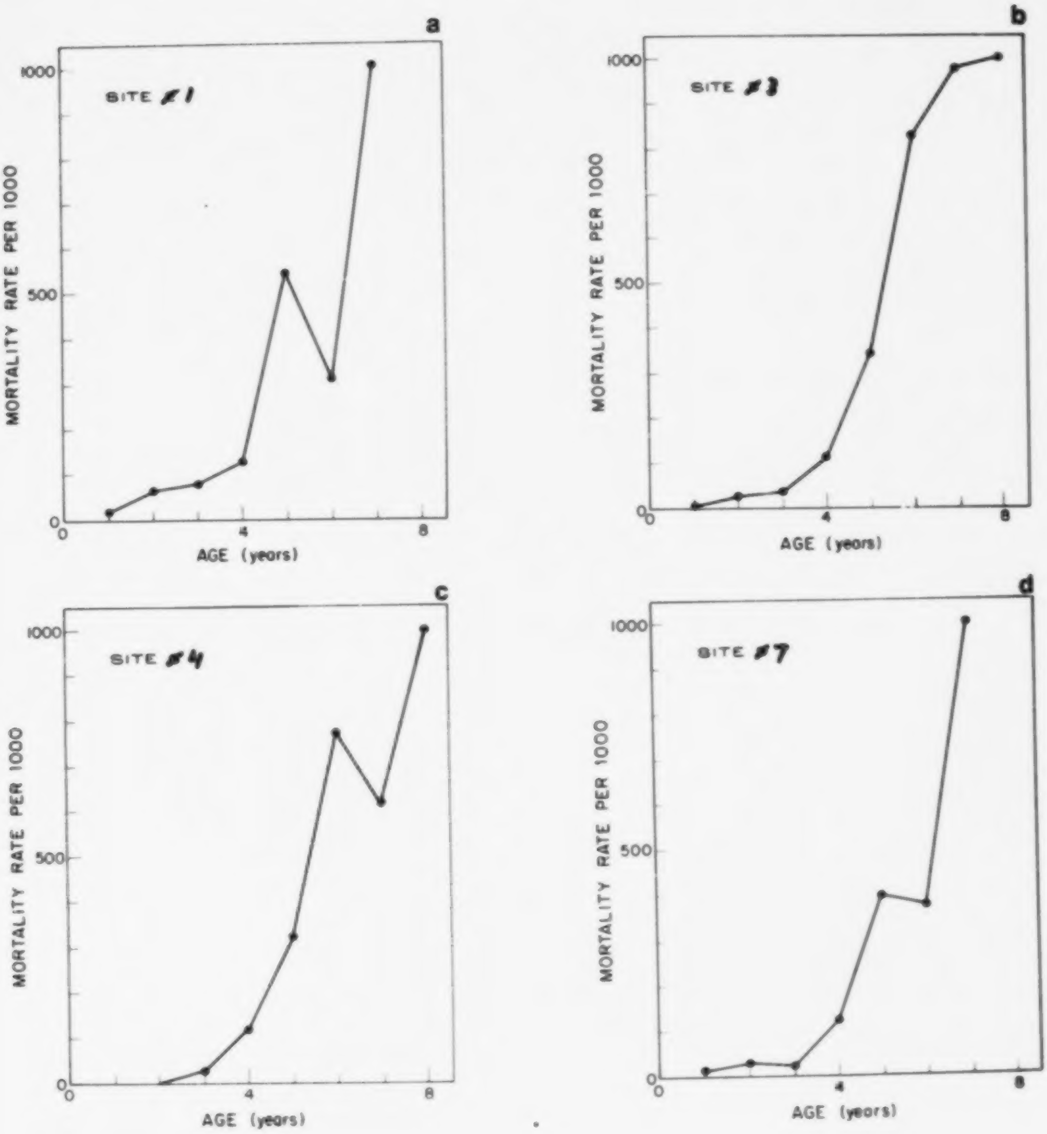


Fig. 6. Death-frequency distributions per season for death assemblages of natural populations of *Mercenaria mercenaria* at sites 1, 3, 4, and 7.



Figs. 7(a-d). Mortality curves for natural populations of Mercenaria mercenaria at sites 1, 3, 4, and 7. Data are presented as mortality per 1000 for each age interval of 1 year (1000 q_x) plotted against the start of the interval.

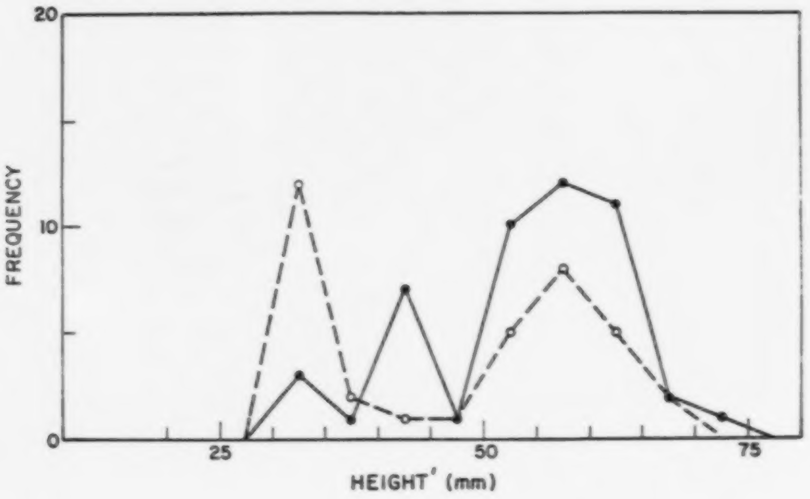


Fig. 8. Size (h')-frequency distributions for death assemblages of transplanted clams recovered from the substratum at sites 1 and 3 in June 1976. (----) Site 1; (——) site 3. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV i.

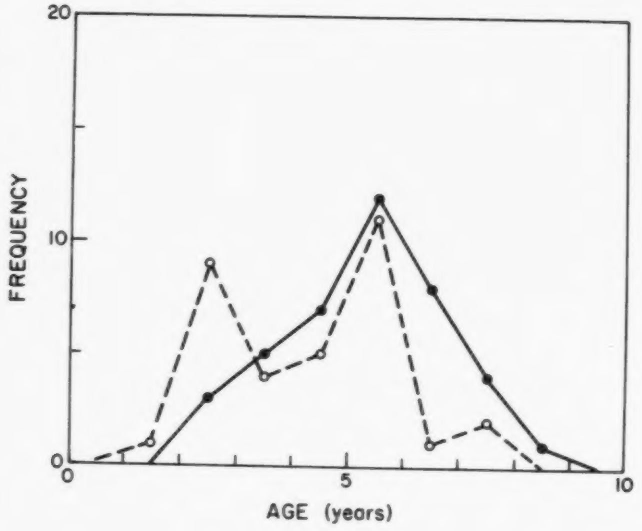


Fig. 9. Absolute age-frequency distributions for death assemblages of transplanted clams retrieved from the substratum at sites 1 and 3 in June 1976. (----) Site 1; (——) Site 3.

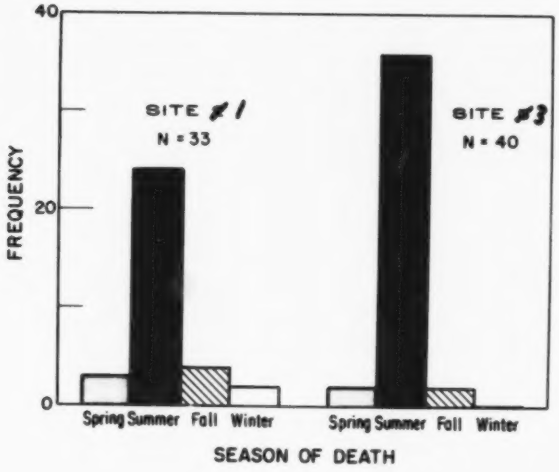


Fig. 10. Death-frequency distributions per season for death assemblages of transplanted clams collected from the substratum at sites 1 and 3 in June 1976.

EXPLANATION OF PLATE I

(a–c) Optical micrographs of acetate peels showing summer microgrowth patterns in the outer shell layer of Mercenaria mercenaria (Linné). Calcium carbonate-rich regions (light bands) represent periods of shell deposition, whereas the organic-rich lines (dark striations) reflect periods of shell dissolution. Note the thick daily growth increments. Scales in a-b equal 100 μm; scale in c equals that in b.

(d–f) Winter microgrowth patterns. Calcium carbonate-rich regions are much thinner than those deposited in the summer (see a-c), indicating that shell growth occurs at a reduced rate during the winter season. Scales in d-e equal that in b; scale in f equals 100 μm.

(g) Bidaily microgrowth pattern. This pattern consists of a couplet; one thick growth increment that follows one thin growth increment (arrows). The couplet forms during a 48-hour period. The cause of this periodicity is unknown. Scale equals that in b.

(h) Subdaily microgrowth pattern. Diffuse organic-rich lines (arrows) occur within daily growth increments. These lines form during intervals of valve closure and shell decalcification within a 24-hour period. Subdaily striations can be distinguished from heavier, daily organic-rich lines. Semidiurnal tides may produce the subdaily microgrowth pattern. Scale equals that in b.

(i) Fortnightly microgrowth pattern. The sequence of thin daily growth increments (n) corresponds to shell growth during neap tide, whereas the series of thick daily growth increments (s) corresponds to shell growth during spring tides. Scale equals 100 μm. (modified from Pannella and MacClintock 1968)

(j) Lunar-monthly microgrowth pattern. Undulations on the outer shell surface (s) reflect a 29-day periodicity. The synodic month causes this microgrowth pattern. Scale equals 500 μm. (modified from Pannella and MacClintock 1968)

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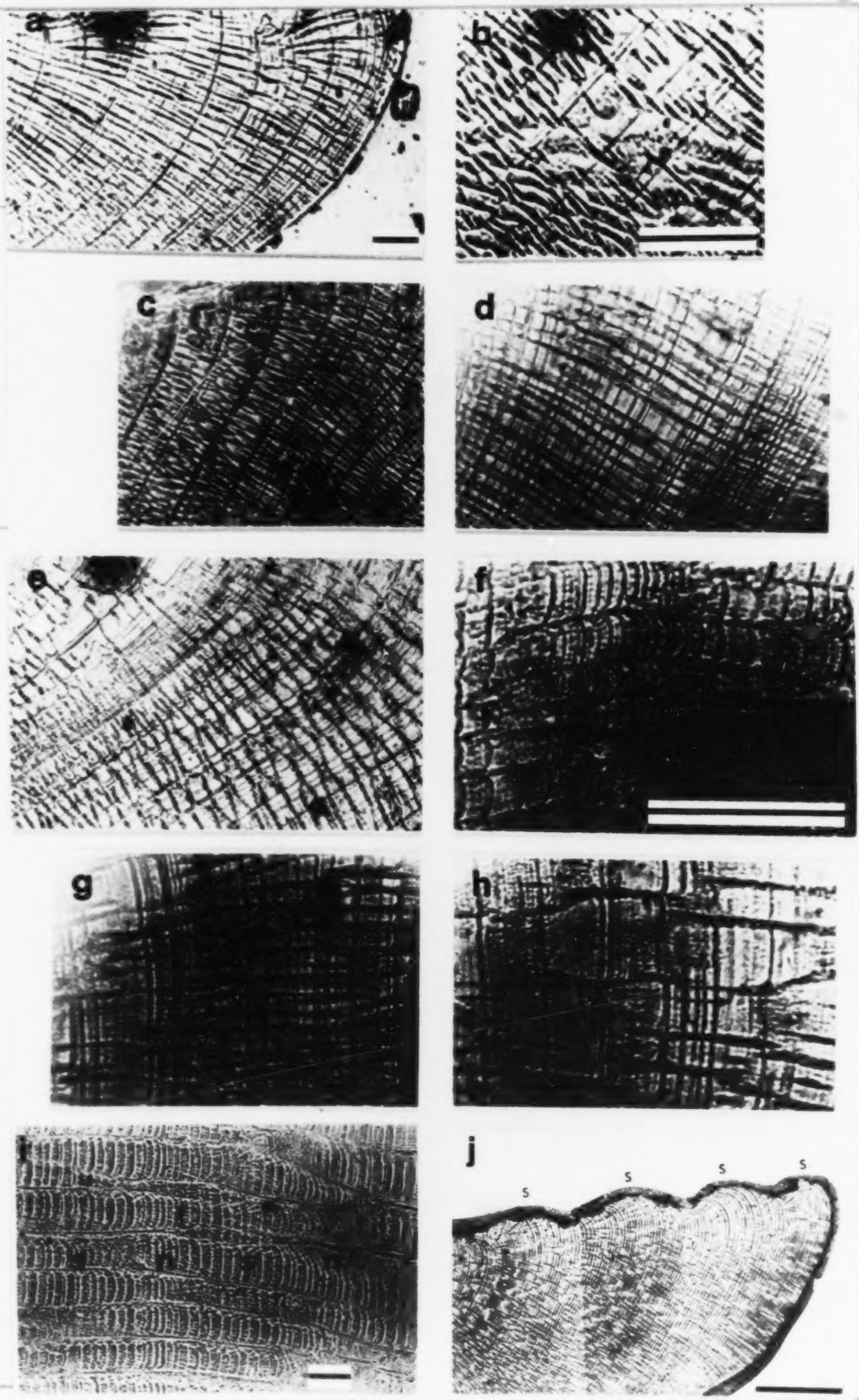

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PLATE I

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EXPLANATION OF PLATE II

(a-c) Freeze-shock breaks. Deep V-shaped notches in the outer shell layer (arrows) are accompanied by thin daily growth increments, crossed-lamellar shell structure, and increased organic material.

(d) Heat-shock break. Thin daily growth increments surround a break in growth (arrow) caused by high water temperatures in the summer. This pattern is structurally similar to the seasonal freeze-shock break (see a-c). Scale equals 100 µm.

(e-g) Thermal-shock breaks. A sudden, but transient temperature change may produce breaks (arrows) delineated by the absence of growth deceleration prior to the breaks. Compare these breaks to those in a-d. Scale in e equals 100 µm; scales in f-g equal that in e.

(h-i) Abrasion breaks. These breaks in growth (arrows) were generated by breaking the periostracal seal at valve margins with fine sandpaper. Shell repair is marked by crossed-lamellar shell structure and thin increments of growth. Scale in h equals 200 µm; scale in i equals 100 µm.

(j) Spawning break. The slight decreases in the thickness of growth increments (horizontal arrows) on both sides of the break (downward pointing arrow) is related to the physiological stress of spawning. Crossed-lamellar shell structure is not associated with the break. Scale equals that in a.

(k) Storm break. Seafloor erosion and high bottom turbidity associated with storms may result in sediment particles becoming trapped between the organism's mantle and shell. These grains can be permanently incorporated into the shell. Note the presence of this break (arrow) with no change in the thickness of growth increments on either side of the break. Scale equals that in a.

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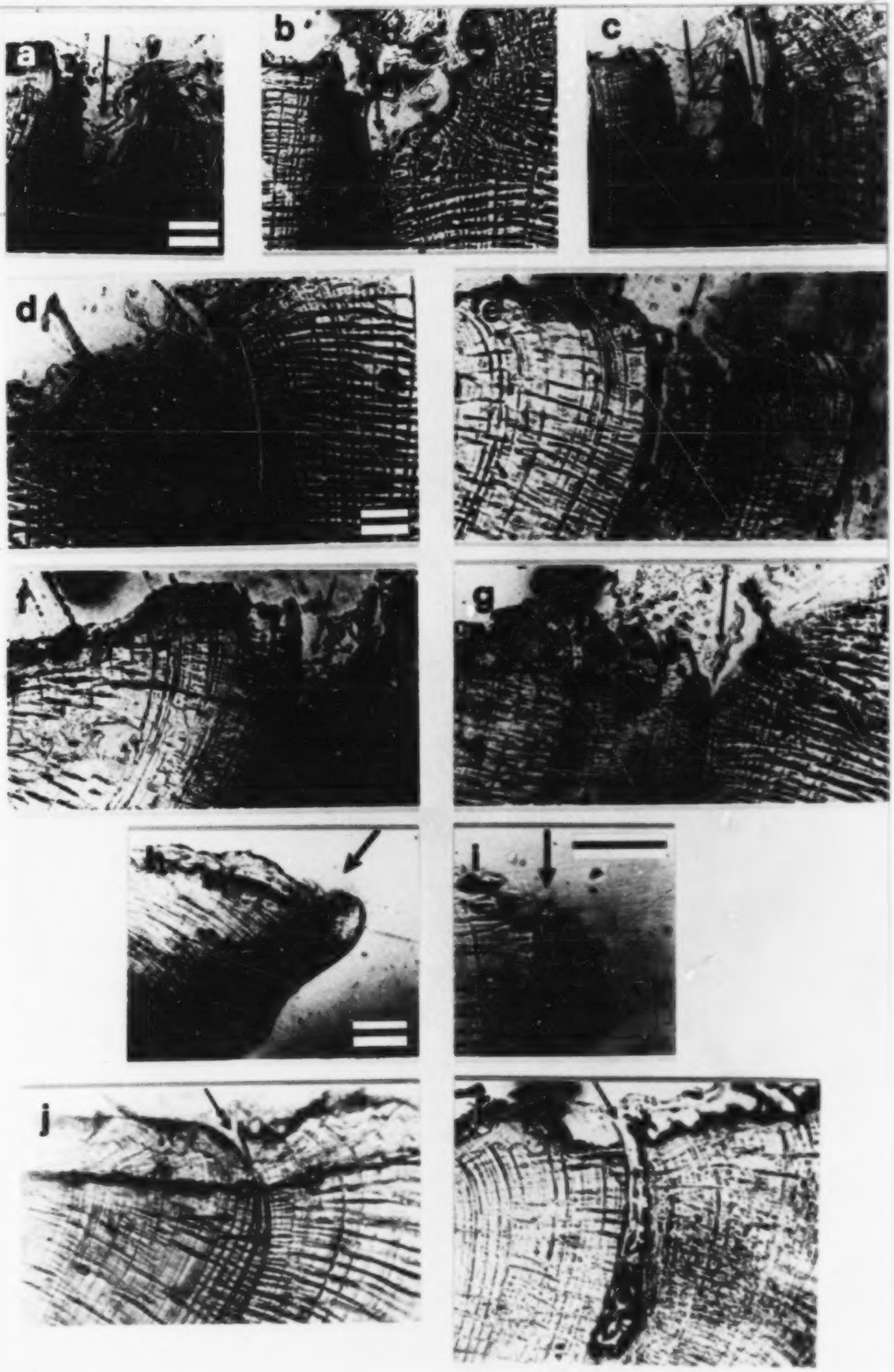

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EXPLANATION OF PLATE III

(a-b) Season of death--early spring. Shell microgrowth patterns near the edge of the shell in specimens that die in the early spring include thin growth increments and growth breaks (arrows) associated with crossed-lamellar shell structure (dark areas). Scale in a equals 200 μm; scale in b equals 100 μm.

(c) Season of death--late spring. Daily growth increments at the shell edge are thicker than those of clams that die in the early spring (see a-b). Crossed-lamellar shell structure is absent. Scale equals that in b.

(d-e) Season of death--summer. Heat-shock breaks (arrows) and crossed-lamellar shell structure occur near the shell margin. Scales equal that in b.

(f-g) Season of death--summer. Spawn breaks located near the shell edge (arrows) were formed during the summer season. Scales equal that in b.

(h) Season of death--summer. A summer storm break (arrow) is near the shell edge. Scale equals that in a.

(i-j) Season of death--summer. Thick daily growth increments diagnostic of rapid summer growth precede the shell margins. Scales equal that in b.

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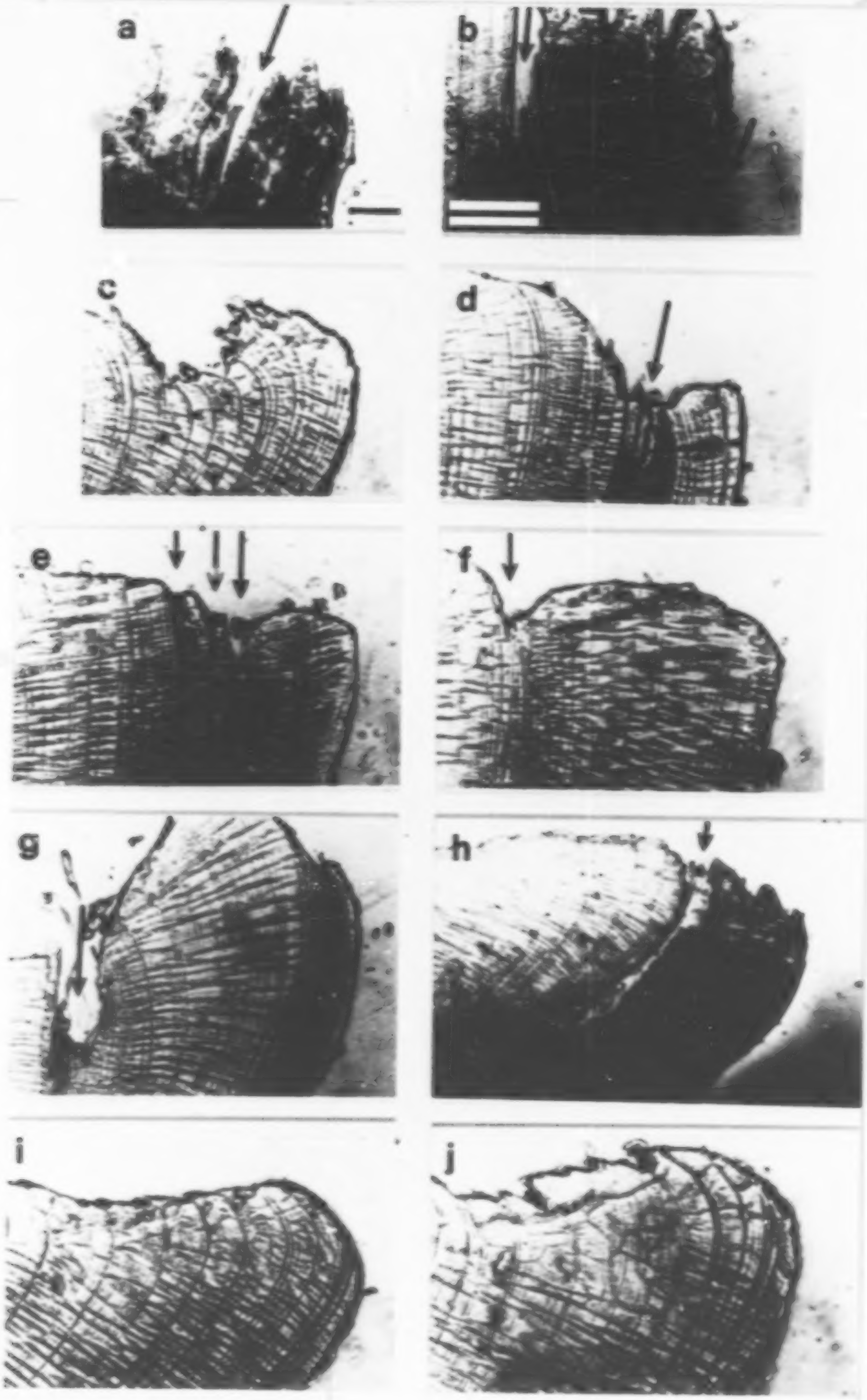

PLATE III

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EXPLANATION OF PLATE IV

(a-d) Season of death--fall. Daily growth increments near the valve margins are of intermediate thickness between those of winter and summer. Fall microgrowth patterns are differentiated from spring patterns by being preceded by summer patterns. A gradual reduction in the thickness of growth increments at the shell margin suggests a moribund condition prior to death. A growth break occurs in micrograph d (arrow). Scale in a equals 100 μm; scales in b-d equal that in a.

(e-h) Winter microgrowth patterns at the ventral valve margins include thin growth increments and freeze-shock breaks (downward pointing arrows). Horizontal arrows point to crossed-lamellar shell structure. Scale in e equals that in a; scales in g and h equal to that in f, 200 μm.

(i) Exterior view of the right-hand valve of the northern quahog, *M. mercenaria*. The solid line represents the true height (h) of the organism. The dashed line denotes the dimension of height (h') used by Kennish (1978). Approximately x0.5.

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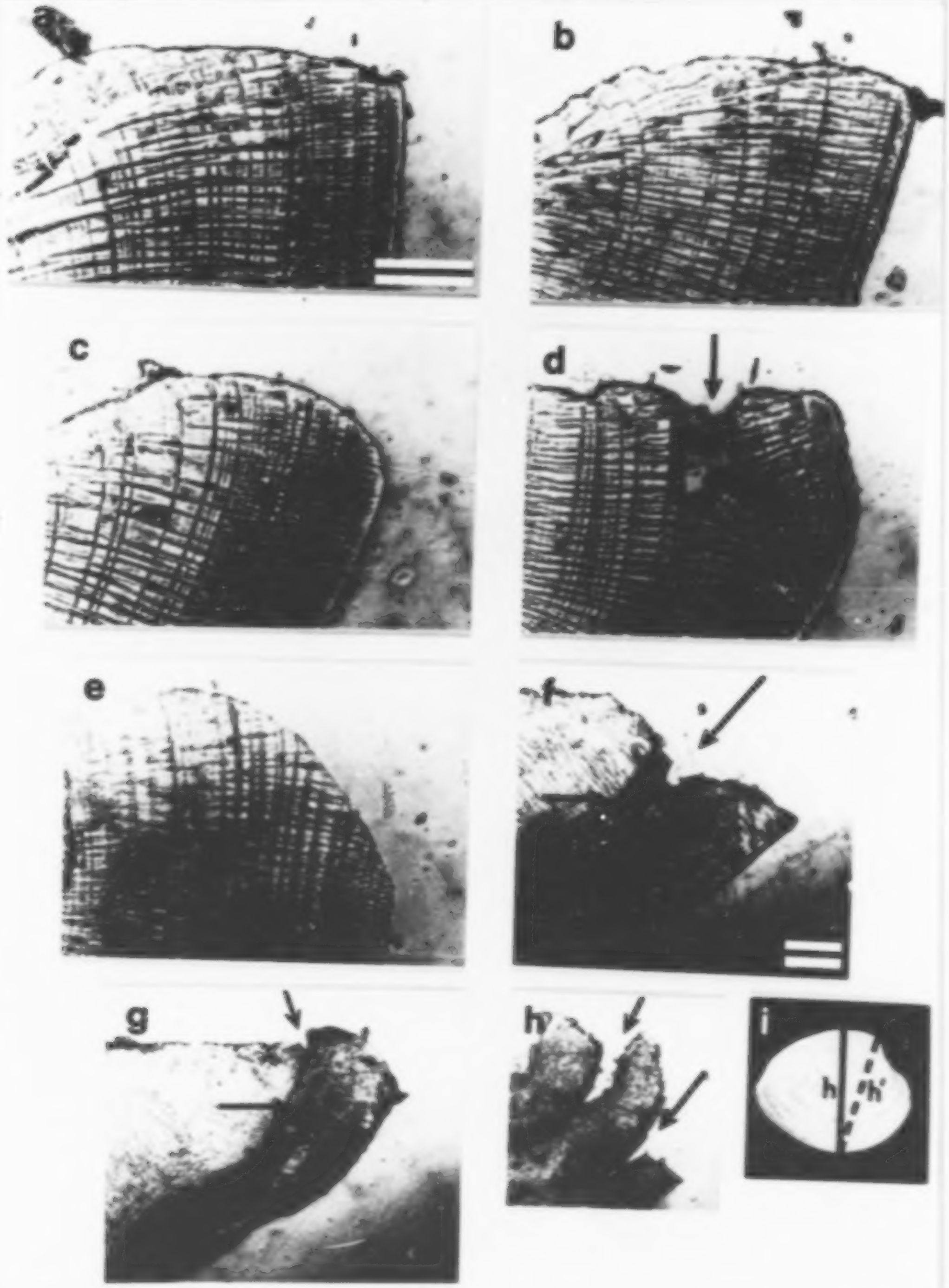

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PLATE IV

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Table 1. Cyclical Microgrowth Patterns in Mercenaria mercenaria (after Kennish and Olsson 1975)

Pattern	Periodicity	Description
Subdaily	<1 day	This pattern is observed as diffuse organic-rich lines surrounded by calcium carbonate-rich regions. The diffuse organic-rich lines form during intervals of anaerobiosis and shell decalcification within a 24-hour period. The calcium carbonate-rich regions form during episodes of shell secretion.
Daily	1 day	A daily growth increment comprises the daily microgrowth pattern. This increment appears as a calcium carbonate-rich region between successive organic-rich lines. In contrast to the diffuse organic-rich lines in the subdaily pattern, diurnal organic-rich lines are well-developed. The daily growth increment forms in response to a circadian locomotor rhythm in the species. When the valves of the organism are open and water is freely pumped, aerobic metabolism occurs and calcium carbonate-rich regions of the shell are deposited. When the valves of the clam are closed, anaerobic respiratory pathways are utilized and shell decalcification occurs, resulting in organic-rich growth lines. This alternating sequence of shell deposition and dissolution takes place on a daily basis.
Bidaily	2 days	A bidaily growth pattern consists of pairs of growth increments--one thick increment that is followed by a thin one. The cause of this couplet is unknown.
Fortnightly	14 days	Fortnightly patterns appear as a cluster of six to eight thin daily growth increments that are followed by a cluster of six to eight thick daily growth increments. Alternating neap and spring tides generate this pattern.
Lunar month	29 days	Monthly patterns are clusters of tidal cycles with an overall periodicity of 29 days. This pattern is manifested on the external shell surface as concentric ridges formed by the thickened outer shell layer. The synodic month produces this pattern.

Table 1. (continued) Cyclical Microgrowth Patterns in *Mercenaria mercenaria* (after Kennish and Olsson 1975)

Pattern	Periodicity	Description
Annual	340-380 days	The yearly cycle is composed of a long sequence of thin daily increments followed by a long sequence of thick daily increments. Seasonal temperature changes are mainly responsible for this cyclical pattern with low winter temperatures yielding thin daily increments and high summer temperatures yielding thick daily increments.

Table 2. Growth Breaks in Mercenaria mercenaria (Kennish and Olsson 1975)

Type of Break	Description
Freeze-shock break	This break is characterized by a deep V-shaped notch in the outer shell layer, and an increase in organic material that extends from the outer layer to the inner homogeneous layer. Daily growth increments gradually decrease in thickness as the break is approached and gradually increase in thickness going away from it. Crossed-lamellar shell structure replaces prismatic shell structure on one or both sides of the break. The gradual decrease of increment thickness approaching the break reflects the gradual decrease in water temperature associated with the onset of winter. The break itself often marks the first freeze of winter, and the gradual increase of increment thickness following the break indicates the slow recovery from the freeze shock. More than one freeze-shock break may be present per winter season.
Heat-shock break	A heat-shock break is structurally similar to a freeze-shock break but is characteristically developed during the summer months. It apparently occurs when the organism is shocked by excessively high water temperatures. More than one heat-shock break may be present per summer season.
Thermal-shock break	A thermal-shock break appears as a sudden break in the normal pattern of growth increment addition. There is usually no slow-down of growth prior to the break, massive slow-down following the break, and transgressing crossed-lamellar shell structure throughout the stressed period. This break was first described in specimens from Barnegat Bay, New Jersey, which were affected by rapid fluctuations in water temperatures associated with sharp changes in operations of the Oyster Creek Nuclear Generating Station.
Abrasion break	An abrasion break is structurally similar to a thermal-shock break but shows less slow-down of growth following the break. Abrasion breaks are frequently produced by filing or sanding the valve margins during transplantation experiments.

Table 2. (continued) Growth Breaks in Mercenaria mercenaria (Kennish and Olsson 1975)

Type of Break	Description
Spawn break	In this break the normal pattern of daily growth increment addition is abruptly interrupted by a break in growth and immediately followed by a sequence of thin, indistinct increments. The sudden occurrence of the break corresponds to the triggering of the spawning event when the proper temperature is attained. The thin increments associated with the break reflect the period during which the clam stops feeding. Transgressing crossed-lamellar shell structure is generally absent.
Neap-tide break	This break in growth is preceded by a rapid decrease in the thickness of growth increments and followed by a rapid increase in the thickness of the growth increments. Such a break, when present, coincides with neap tides. Crossed-lamellar shell structure is usually absent.
Storm break	A storm break appears as a break in the normal depositional pattern of shell growth which is abruptly followed by recovery. The thickness of growth increments prior to and following the break is not significantly altered. Silt grains are occasionally incorporated into the outer shell layer. Crossed-lamellar shell structure is generally lacking.

Table 3. Size statistics for life and death assemblages of *Mercenaria mercenaria* in Barnegat Bay. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV i.

		Life assemblage				Death assemblage			
Site Fig. 4	Year	No. of clams	Mean height'(mm) ±95% C.I.	Std. dev. for mean	Median height' (mm)	No. of clams	Mean height'(mm) ±95% C.I.	Std. dev. for mean	Median height' (mm)
1	1974	no data				405	51.75±1.06	10.81	54.50
3	1974	no data				446	55.38±0.74	7.91	57.00
4	1974	no data				464	55.89±0.73	7.97	56.50
7	1974	no data				261	60.47±1.29	10.56	62.00
1	1976	435	54.56±0.75	7.97	55.20	499	53.36±0.76	8.69	54.45
2	1976	342	50.33±0.91	8.52	49.60	280	54.16±1.11	9.47	55.48
3	1976	446	51.07±0.78	8.38	49.45	445	59.17±0.78	8.37	60.60
4	1976	441	51.24±0.88	9.41	52.70	408	56.45±0.87	8.95	57.80
5	1976	416	11.84±0.37	3.85	11.10	16	17.52±3.44	6.45	16.85
6	1976	450	52.52±0.70	7.54	52.63	413	57.78±1.02	10.53	57.80
7	1976	436	56.26±0.63	6.64	56.25	214	55.25±1.30	9.63	56.30
8	1976	440	54.24±0.70	7.51	53.77	436	54.62±0.84	8.89	55.60
9	1976	208	54.20±1.04	7.63	55.00	438	57.27±0.85	9.07	58.60

Table 4. Age-height' statistics for samples of clams from sites 1, 3, 4, and 7. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV i.

Site	No. of clams	Mean height' (mm)	Std. dev.	Mean age (yrs)	Std. dev.
1	101	43.12	12.81	3.92	1.70
3	74	46.82	12.57	4.25	1.72
4	64	49.74	9.65	5.03	1.31
7	38	46.82	17.05	4.03	1.79

Table 5. Mean age-height' relationships observed in death assemblages of clams at sites 1, 3, 4, and 7. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV 1.

	Site 1, N* = 101			Site 3, N* = 74			Site 4, N* = 64			Site 7, N* = 38		
Age	N**	Mean height' (mm)	Std. dev.	N**	Mean height' (mm)	Std. dev.	N**	Mean height' (mm)	Std. dev.	N**	Mean height' (mm)	Std. dev.
1	101	12.39	3.76	74	11.36	4.16	64	7.04	2.71	38	12.72	5.15
2	89	23.00	4.49	68	23.51	4.96	64	17.70	4.24	35	25.61	6.19
3	65	32.91	4.49	63	35.01	4.89	63	29.54	5.22	25	37.30	6.42
4	50	42.36	5.26	44	43.78	4.15	54	39.55	5.23	19	46.97	5.25
5	28	49.37	6.27	19	49.89	3.01	28	47.75	5.81	12	55.58	7.05
6	16	57.61	7.76	9	56.18	3.94	10	55.11	4.05	6	62.13	8.88
7	6	59.52	5.41	6	63.60	1.70	7	63.30	4.56	3	65.80	3.04
8	0	—	—	4	70.60	1.75	3	69.13	5.95	0	—	—

N* = number of clams

N** = number of size measurements per age

Table 6. Mean age-height' relationships for the pooled death assemblages of clams from sites 1, 3, 4, and 7. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV i.

		N* = 277	
Age	N**	Mean height' (mm)	Std. dev.
1	277	10.92	4.44
2	256	22.17	5.51
3	216	33.05	5.67
4	167	42.35	5.47
5	87	49.82	6.11
6	41	57.35	6.65
7	22	62.69	4.37
8	7	69.97	3.73

N* = number of clams

N** = number of size measurements per age

Table 7. Death-frequency distributions per season for natural populations of *Mercenaria mercenaria* at sites 1, 3, 4, and 7.

		Season of death			
Site	No. of clams	Spring	Summer	Fall	Winter
1	101	12 (11.88%)	33 (32.67%)	25 (24.75%)	31 (30.69%)
3	75	13 (17.33%)	24 (32.00%)	13 (17.33%)	25 (33.33%)
4	64	13 (20.31%)	19 (29.69%)	12 (18.75%)	20 (31.25%)
7	38	9 (23.68%)	16 (42.11%)	7 (18.42%)	6 (15.79%)
all sites	278	47 (16.91%)	92 (33.09%)	57 (20.50%)	82 (29.50%)

*Percentage of mortality per season in parentheses

Table 8. Life table for *Mercenaria mercenaria* at site 1.

Age interval x to x + 1 years	Proportion dying in interval (x, x + 1)	Number living at age x	Number dying in interval (x, x + 1)	Number of time-spans lived in interval (x, x + 1)	Total number of time-spans lived past age x	Average life expectancy (in years) at age x	Proportion surviving in interval (x, x + 1)
	$1000\ q_x$	l_x	d_x	L_x	T_x	e_x	p_x
1-2	22.00	1000	22	989.0	4508.0	4.5080	0.9780
2-3	68.51	978	67	944.5	3519.0	3.5982	0.9315
3-4	83.42	911	76	873.0	2574.5	2.8260	0.9166
4-5	130.54	835	109	780.5	1701.5	2.0377	0.8695
5-6	544.08	726	395	528.5	921.0	1.2686	0.4559
6-7	314.20	331	104	279.0	392.5	1.1858	0.6858
7-8	1000.00	227	227	113.5	113.5	0.5000	0.0000

Table 9. Life table for Mercenaria mercenaria at site 3.

Age interval x to x + 1 years	Proportion dying in interval (x, x + 1)	Number living at age x	Number dying in interval (x, x + 1)	Number of time-spans lived in interval (x, x + 1)	Total number of time-spans lived past age x	Average life expectancy (in years) at age x	Proportion surviving in interval (x, x + 1)
	$1000\ q_x$	l_x	d_x	L_x	T_x	e_x	p_x
1-2	7.00	1000	7	996.5	4844.0	4.8440	0.9930
2-3	27.19	993	27	979.5	3847.5	3.8746	0.9728
3-4	39.34	966	38	947.0	2868.0	2.9689	0.9607
4-5	113.15	928	105	875.5	1921.0	2.0700	0.8869
5-6	343.86	823	283	681.5	1045.5	1.2704	0.6561
6-7	829.63	540	448	316.0	364.0	0.6741	0.1704
7-8	978.26	92	90	47.0	48.0	0.5217	0.0217
8-9	1000.00	2	2	1.0	1.0	0.5000	0.0000

Table 10. Life table for *Mercenaria mercenaria* at site 4.

Age interval x to x + 1 years	Proportion dying in interval (x, x + 1)	Number living at age x	Number dying in interval (x, x + 1)	Number of time-spans lived in interval (x, x + 1)	Total number time-spans lived past age x	Average life expectancy (in years) at age x	Proportion surviving in interval (x, x + 1)
	$1000\ q_x$	l_x	d_x	L_x	T_x	e_x	p_x
1-2	0.00	1000	0	1000.0	5074.0	5.0740	1.0000
2-3	0.00	1000	0	1000.0	4074.0	4.0740	1.0000
3-4	30.00	1000	30	985.0	3074.0	3.0740	0.9700
4-5	122.68	970	119	910.5	2089.0	2.1536	0.8773
5-6	324.32	851	276	713.0	1178.5	1.3848	0.6757
6-7	775.65	575	446	352.0	465.5	0.8096	0.2244
7-8	620.16	129	80	89.0	113.5	0.8798	0.3798
8-9	1000.00	49	49	24.5	24.5	0.5000	0.0000

Table 11. Life table for Mercenaria mercenaria at site 7.

Age interval x to x + 1 years	Proportion dying in interval (x, x + 1)	Number living at age x	Number dying in interval (x, x + 1)	Number of time-spans lived in interval (x, x + 1)	Total number of time-spans lived past age x	Average life expectancy (in years) at age x	Proportion surviving in interval (x, x + 1)
	1000 q_x	l_x	d_x	L_x	T_x	e_x	p_x
1-2	19	1000	19	990.5	4951.0	4.9510	0.9810
2-3	34.66	981	34	964.0	3960.5	4.0372	0.9653
3-4	24.29	947	23	935.5	2996.5	3.1642	0.9757
4-5	124.46	924	115	866.5	2061.0	2.2305	0.8755
5-6	398.02	809	322	648.0	1194.5	1.4765	0.6020
6-7	377.82	487	184	395.0	546.5	1.1222	0.6222
7-8	1000.00	303	303	151.5	151.5	0.5000	0.0000

Table 12. Size (height')-frequency distributions for clams transplanted to the substratum at sites 1 and 3 in June 1975. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV 1.

Size class (mm)	Frequency of clams transplanted to site 1	Frequency of clams transplanted to site 3
20-25	1	0
25-30	9	10
30-35	103	103
35-40	69	68
40-45	116	117
45-50	115	114
50-55	124	124
55-60	103	103
60-65	66	67
65-70	24	24
70-75	10	10
75-80	3	3
	N* = 743	N* = 743

N* = total number of clams

Table 13. Size (height')-frequency distributions for live and dead clams recovered from the substratum at sites 1 and 3 in June 1976. Clams originally transplanted in June 1975. Height' represents a dimension of the shell from the umbo to the ventral margin at a slight angle to the dorso-ventral plane. See Plate IV i.

Size class (mm)	Frequency of live clams recovered from site 2	Frequency of dead clams recovered from site 2	Frequency of live clams recovered from site 5	Frequency of dead clams recovered from site 5
20-25	0	0	0	0
25-30	0	0	0	0
30-35	11	12	20	3
35-40	43	2	31	1
40-45	86	1	73	7
45-50	104	1	90	1
50-55	97	5	62	10
55-60	113	8	64	12
60-65	49	5	44	11
65-70	11	2	12	2
70-75	1	0	2	1
75-80	0	0	0	0
				+3 (broken)
	N* = 515	N* = 36	N* = 398	N* = 51

N* = total number of clams

ACKNOWLEDGMENTS

Financial support for the author's research reported in this chapter was kindly provided by the Geological Society of America, the Society of Sigma Xi, the Marine Sciences Center of Rutgers University, and the Jersey Central Power & Light Company.

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CHAPTER 4

ECOLOGICAL AND PALEONTOLOGICAL INTERPRETATION OF LARVAL SHELL MORPHOLOGY

by

David Jablonski* and Richard A. Lutz

Department of Geology and Geophysics
Yale University
New Haven, Connecticut
06520

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*Present address: Department of Geological Sciences, University of California, Santa Barbara, California 93106

CHAPTER 4

I. INTRODUCTION

Considerable information is contained within the molluscan shell on the ontogenetic history of the organism. In this chapter, we are concerned with the earliest calcified portion of the shell, that secreted by larvae and young juveniles. Careful interpretation of the morphological features of the shell apex or umbo region can provide insight into molluscan systematics, ecology, biogeography, and evolution (e.g. Thorson 1950; Scheltema 1971a, b, 1977, 1978, 1979a, b; Thiede 1974; Kauffman 1975; Lutz 1977; Jablonski 1978a, 1979; Hansen 1978a, b; Jablonski and Lutz 1978; Lutz and Jablonski 1978a, b, c, 1979; Hansen and Jablonski 1979).

II. DEVELOPMENTAL TYPES IN MARINE BENTHIC INVERTEBRATES

Many classifications have been proposed for the spectrum of developmental types found in marine benthic invertebrates (cf. Mileikovsky 1974a). The classification employed depends largely on the perspective of the individual investigator. For example, a paleobiogeographer concerned with dispersal capability might emphasize the dichotomy between those larvae which feed during the pelagic state and those which do not (planktotrophy *vs.* nonplanktotrophy). Alternatively, such a worker might wish to classify larval forms according to their swimming capabilities (pelagic *vs.* nonpelagic). A population ecologist might finely subdivide developmental types according to amount of reproductive effort invested by the parent, while an embryologist might be more interested in the presence or absence of a distinct larval state (direct *vs.* indirect development). In the present study, we adopt an informal classification of general utility, a modified version of that devised by Thorson (1946, 1950) in the course of his monumental work on marine larval ecology. In such a classification scheme, the various types of larval development fall under two main categories: planktotrophic and nonplanktotrophic larvae. We stress this dichotomy in feeding type because it is readily recognizable using shell morphology, and because planktotrophic larvae may have a prolonged pelagic stage and thus high dispersal capability. Nonplanktotrophic larvae may be pelagic or nonpelagic, and in either case will generally have lower dispersal capability than planktotrophs. This classification, which is briefly discussed in the following paragraphs, is not all-encompassing; intergradations, exceptions, and combinations of two or more developmental types within a single life cycle render the presented scheme as artificial as any other simple pigeonholing of the complexity of the natural world.

Planktotrophic Larvae

Pelagic larvae spend a significant portion of their development time in surface waters as free-swimming veligers. Planktotrophic pelagic larvae depend on smaller planktic organisms (and possibly organic detritus) for nutrition during the pelagic stage. This involves development of complex structures which function in locomotion and feeding (Figs. 1,2), all of which are lost or resorbed during metamorphosis when the larva settles and assumes a benthic mode of life. Eggs are released virtually yolk free, and thus there is a minimum expenditure per egg per parent. Species having planktotrophic larvae produce them in great numbers--up to 70 million eggs per individual in a single spawning of the oyster *Crassostrea virginica* [see Davis and Chanley (1966)], and 2.5-25 million eggs per individual per spawning in the abalone *Haliotis midae* [see Newman (1967)]. Most gastropods, however, produce fewer eggs [see Webber (1977), Table IX)]. However, predation, starvation, and other mortality factors take a tremendous toll of planktotrophic larvae before and just after settlement (over 99% mortality; Thorson 1950, 1966; Mileikovsky 1971).[1] In spite of this extremely high larval mortality, the enormous numbers of pelagic larvae produced by populations of planktotrophic species are sufficient to ensure dispersal and survival. For example, Ayers (1956) calculated that only 0.0013% of the larvae need survive annually to maintain a population of *Mya arenaria* in Barnstable Harbor, Massachusetts.

Scheltema (1967) divided the pelagic stage of planktotrophic species into two phases: (1) growth and development, followed by (2) a "delay period," in which development is essentially completed, but a final loss of pelagic adaptations is postponed until a substratum suitable for settlement is found. Scheltema (1971a, p. 306) further comments that "it is the delay period which gives to many species the greatest flexibility in the length of their larval life," since this stage may last from a few minutes to over three months, depending on the species.[2] The complex process of selection of settlement sites is reviewed by Meadows and Campbell (1972a, b), Scheltema (1974) and Crisp (1974), and has been modeled as an absorbing Markov chain by Doyle (1975, 1976).

The ability to subsist on planktic food not only obviates the need for deposition of yolk (in the egg) as an energy source for the developing larvae, but also allows a long pelagic larval duration for many species. The evolutionary success of this mode of development is indicated by Thorson's (1950; see also Mileikovsky 1971) estimate that 70% of all benthic marine species undergo planktotrophic development. In temperate-water species, this pelagic stage generally lasts from 2 to 6 weeks (Thorson 1961); Scheltema (1977) has pointed out that during this period an ocean current of only 0.5 km/hr could carry a larva 150-550 km. Other species, notably among the tropical benthos, can remain in the plankton for 6 months or more, and thus may be carried great distances by ocean currents. Larvae of this type have been termed teleplanic (Gr. *teleplanos*, "far-wandering", Scheltema 1971b) larvae. Scheltema (1971a, 1977) discussed several tropical gastropod species having larvae capable of traversing trans-oceanic distances, and thus maintaining the amphi-Atlantic distribution of the adults (see also Edmunds 1977). The ecological and evolutionary implications of a long pelagic stage in essentially sessile benthic organisms will be considered in more detail later in this chapter.

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[1] The actual sources of larval mortality are poorly known. Thorson (1950), Mileikovsky (1971, 1974b), and many others have emphasized the impact of predation. Laboratory studies (e.g. Loosanoff 1954; Bayne 1965; Millar and Scott 1967) have led to suggestions concerning the role of larval starvation, but as Thorson (1950) points out, planktotrophic larvae found in nature rarely, if ever, exhibit the characteristics of starved laboratory specimens. However, because level of food availability (in addition to temperature and a number of other factors; e.g. Bayne 1965) may markedly affect growth rates, starvation may indirectly contribute to larval mortality by significantly prolonging the pelagic larval stage and thus the amount of time the larvae are exposed to predation (Vance 1973a, b).

[2] If this delay period is extended beyond a certain limit, for example, by depriving larval cultures of a suitable settlement substratum, the larvae can lose their ability to metamorphose (e.g. in asteroids, Barker 1977).

Demersal larvae undergo development while swimming and/or crawling in the near-bottom water layer, apparently feeding on organic detritus (or bacteria?) in the water close to or on the sediment. Some benthic feeding may occur, and inclusion of this larval type within the general planktotrophic category may be incorrect. Though poorly documented, this mode of development is probably an important one in high-latitude and deep-sea faunas (Pearse 1969; Mileikovsky 1971). Demersal development has been demonstrated in a number of polar echinoderms (Pearse 1965, 1969; Pearse and Giese 1966), but, apparently, in only a few molluscan species, notably the olivid gastropod, *Olivella verreauxi* (Radwin and Chamberlin 1973), and perhaps in *Hydrobia ulvae* (Fish and Fish 1974, p. 696; see also Fish and Fish 1977). In high latitudes, this dispersal mode appears to be an adaptive compromise, retaining some of the advantages of pelagic larvae, while reducing mortality by keeping larvae out of the polar surface waters (Pearse 1969). Also, benthic dispersal may expose larvae to a more stable benthic food resource compared to the seasonally variable production at the sea surface (cf. Levinton 1974; McCall 1978).

Nonplanktotrophic Larvae

Lecithotrophic larvae are nourished by the yolk of the eggs from which they develop (and are thus nonplanktotrophic). Such larvae are either entirely non-pelagic or remain in the plankton for little more than a few hours to a few days (Thorson 1950, 1961).[3] Clearly, reproductive effort per offspring is much higher, and larval mortality much lower, than in planktotrophic species. Accordingly, far fewer eggs per parent are produced [4100 eggs per parent in the bivalve *Nucula proxima* and 1200 in the related species *N. annulata*, see Scheltema (1972)].

In contrast to species having lecithotrophic larvae with a pelagic phase, oviparous species have lecithotrophic larvae which develop entirely within an egg mass or egg case (often attached to a hard substratum). Embryos pass through a lecithotrophic veliger stage, with metamorphosis taking place within the protection of the egg mass. The offspring emerge as juveniles (i.e. miniature adults); for example, Nucula delphinodonta (Drew 1901). This mode of reproduction has been termed direct development (Thorson 1946, 1950; Mileikovsky 1971, 1974; Webber 1977), but as Chia (1974) emphasized, this term should be applied only to species that do not pass through a distinct intermediate stage such as a veliger. Direct development should apply only to the embryos (which may or may not be free-living) that morphologically differentiate gradually into the adult. Certain opisthobranchs (Bonar 1978, who uses the term ametamorphic development), most cephalopods (e.g. Arnold and Williams-Arnold 1977; Wells and Wells 1977; Boletzky 1974) and some echinoderms (Chia 1974) show true direct development.

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[3] A remarkable exception to this general observation is the lecithotrophic sea-star *Mediaster aequalis*, which begins settling at approximately 30 days. Under laboratory conditions, though probably not natural conditions, this species is capable of delaying metamorphosis for up to 14 months, apparently without feeding (Birkeland et al. 1971).

Among the higher prosobranch gastropods (Neogastropoda), oviparous species may deposit, along with viable eggs, a supplementary food source in the form of nurse eggs. The ratio of nurse eggs to viable eggs may vary considerably within a species. For example, the gastropod Buccinum undatum deposits 50-2,000 eggs per capsule, with only 10-30 of these eggs developing into juveniles (Portmann 1925; see Webber 1977, for a tabulation of prosobranch data). Spight (1976) has shown that embryos feeding on nurse eggs show a greater range in hatching size than embryos in which the entire yolk supply is enclosed within their own egg membrane (see also Fioroni 1966, 1977).

Brooded larvae, characteristic of ovoviviparous species, are retained (sometimes encapsulated) within the parent throughout development, emerging as metamorphosed juveniles. Thus ovoviviparous species can be regarded as investing the greatest amount of effort into the protection of their offspring during early ontogeny. This developmental type has been termed viviparity (Thorson 1946, 1950; Mileikovsky 1971, 1974a), but Simpson (1977, p. 128) writes:

> "a viviparous condition requires that the developing embryo derives nutriment by close contact with maternal tissues without interposition of egg membranes, for example, as in placental mammals. Surely this must not be the case for the invertebrates frequently listed as viviparous in the literature. Ovoviviparous is the correct term in describing embryos that develop within the maternal organism from which they derive nutriment but are separated from the parent organism by egg membranes for most or all of their development, which is at the expense of yolk. It is an important distinction."

Purchon (1968, p. 307-312) cites a number of examples which might be regarded as intermediate between ovoviviparity and oviparity, in which eggs are attached, and developing embryos are carried, on the surface of the shell or on the body of the parent. Such developing embryos might be placed, somewhat arbitrarily, in the general category of brooded larvae.

III. RECOGNITION OF DEVELOPMENTAL TYPES FROM LARVAL SHELL MORPHOLOGY

One of the fundamental dichotomies in larval adaptation, the presence or absence of a yolky food supply during development (nonplanktotrophy vs. planktotrophy) affects egg size, which is reflected in the morphology of the larval shell. Thus, the study of both larval and well-preserved early juvenile molluscan shells permits inferences to be made concerning developmental types of extant, or even long-extinct, species.

Gastropoda

Terminology. A number of different terminologies have been erected for the early stages of gastropod shell growth. Here we follow Thiriot-Quiévreux (1972) and Robertson (1974) in designating the protoconch as the entire shell formed prior to metamorphosis [following Robertson (1974), we consider this term synonymous with "larval shell"] (Fig. 3). Protoconch I, the "embryonic shell" of Fretter (1967) and Robertson (1971) is the initial shell, comprising less than two whorls, or even less than one whorl in some species, reportedly secreted by the shell gland while the embryo is still enclosed within the egg membrane (Raven 1966). It is generally unornamented, except for granulations and striae, which are apparently loci of shell deposition. Protoconch II is deposited by the mantle edge during the veliger stage and ranges from 1½ to 8 smooth to heavily ornamented whorls. The ornamentation pattern may not be the same on all of the whorls and may not be consistent with the adult ornamentation (e.g. Fig. 3). The ultrastructure of the protoconch has not been described in detail; Togo (1977) reported simple prismatic structure and "irregularly complex" structure (disordered aragonite needles) in the archaeogastropod Haliotis, and a "protocrossed lamellar" structure in eight neogastropod species. The teleoconch (sometimes misspelled "teloconch") is the post-larval shell, laid down after metamorphosis (Fig. 3).

Because protoconchs are rarely planispiral, it is difficult to accurately define the number of whorls present. We prefer the method used by Taylor (1975). A line is drawn from the sutural point of the aperture perpendicular to and across the remaining apical sutures. The sutural point at the aperture is counted as one complete whorl; another whorl is added to the count each time the perpendicular line is crossed (Fig. 4).

Criteria. The key character in distinguishing between planktotrophic and nonplanktotrophic larval shells was indicated in Thorson's (1950, p. 33) "apex theory" [also well-articulated by Powell (1942)] which states that "as a general rule, a clumsy, large apex points to a nonpelagic development, while a narrowly twisted apex, often with delicate sculpture, points to a pelagic development." That is, large rounded, often paucispiral protoconchs indicate larvae which spend little or no time in the plankton, while narrow, polygyrate protoconchs suggest planktotrophic larvae (see also Shuto 1974). Thorson (1950) himself, as well as subsequent authors (e.g. Robertson 1974; Taylor 1975), suggested caution in utilizing this character, as numerous exceptions are known.[4]

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[4] Thorson (1950) states, 'As, however, the notion 'a clumsy or a narrowly

With the increasing application of the scanning electron microscope (SEM) to larval shell studies (e.g. Fretter and Pilkington 1971; Robertson 1971; Richter and Thorson 1975; Bouchet 1976), a more precise criterion, with a closer direct relationship to the underlying development process, can be used. A small Protoconch I (boundary readily discernable using the SEM) generally derives from a small (60-200 µm), yolk-poor egg; larval development is generally planktotrophic (Fig. 5A). In contrast, larval shells in which the whorl has a large diameter and which lack a sharply demarcated Protoconch I grow from large, probably yolk-rich eggs; larval development is generally nonplanktotrophic (Robertson 1971, 1974; Rodriguez Babio and Thiriot-Quiévreux 1974; Shuto 1974; Marshall 1978) (Fig. 5B). The direct relationship between egg size and hatching size (and, thus, developmental type) has been investigated quantitatively by Amio (9163), Fioroni (1966), Shuto (1974), and Spight (1976b); for discussion of the more controversial relationship between egg size and developmental time, see Underwood (1974a), Vance (1974), Strathmann (1977), and Steele (1977). Simpson (1977) has shown that the relationship between developmental type and egg size can be used to predict mode of development from examination of the ovaries.

Shuto (1974) has made some empirical observations concerning correlations between protoconch morphology and mode of larval life. The ratio of the maximum diameter (D; in mm) to the number of whorls or volutions (Vol) was found to be greater than 1.0 for species with lecithotrophic larvae (Fig. 6). Most protoconchs with D/Vol between 0.3 and 1.0 and less than 2.25 volutions also belong to species having lecithotrophic larvae, while larvae of species with D/Vol values less than 0.3 and with more than 3 volutions are generally planktotrophic [see also Sohl (1977) for a discussion of the relationship between Vol and length of pelagic life]. D/Vol values between 0.3 and 1.0 and with less than 3 volutions are found in species with planktotrophic larvae, as well as those with lecithotrophic larvae.

Shuto (1974) also considered certain types of protoconch ornamentation, such as close brephic axials and fine cancellate and reticulate ornamentation, to be indicative of planktotrophy (Fig. 7). Such ornamentation probably serves to strengthen the shell against the rigors of a more or less prolonged free-swimming interval (see also Bandel 1975a). A sinusigera lip on the larval aperture (evident in later life as the protoconch-teleoconch boundary) accommodates the extended velar lobes of the larva and is best developed in teleplanic larvae (see also Robertson 1974).

Finally, the most dependable method of distinguishing planktotrophic from nonplanktotrophic developmental types in gastropods is the approach advocated by Scheltema (1978, 1979a, b). In order to assess the mode of development, protoconchs of a given species should be compared to those of a congeneric or confamilial species whose developmental characteristics are

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twisted apex' is different in large and tiny adult shells and may even be different in temperate and tropical genera. . . . a general rule valid for all apices cannot be given. Only when we know the type of apex derived from a pelagic or a non-pelagic development with the individual genus, can reliable results be obtained."

known. At these taxonomic levels, congruence of shell morphology probably indicates similarity of developmental history.[5] Even this is not an infallible technique; Robertson (personal communication 1979) reports that planktotrophic and lecithotrophic Boonea (Pyramidellidae) have identical protoconchs.

Identification of larval gastropods (both living and fossil) is difficult because few species have been adequately described, and most published studies deal exclusively with newly-hatched larvae. Some important papers that describe later pelagic veliger stages include: Thorson (1946); Lebour (1936, 1937, 1945); Natarajan (1957); Fretter and Pilkington (1970); Pilkington (1974, 1976); and Taylor (1975).

Although some gastropods appear to have species-specific protoconch morphologies, identification of larval or early juvenile shells must generally be based on careful comparison with the apexes of metamorphosed juveniles which have attained an age at which diagnostic shell features are available. The protochonch is often abraded from adult specimens, so it is often necessary to assemble growth series. Excellent figures for comparative purposes have been presented in a number of SEM studies (e.g. Richter and Thorson 1975; Bandel 1975a, b; Rodriguez Babio and Thiriot-Quiévreux 1074, 1975; Thiriot-Quiévreux and Rodriguez Babio 1975; Jung 1975).

Taxonomic distribution. The taxonomic distribution of developmental types in prosobranch gastropods has been reviewed by Anderson (1960), Fretter and Graham (1962), Radwin and Chamberlin (1973), Taylor (1975), and Webber (1977). The following discussion is abstracted from these much more extensive surveys.

Archaeogastropods typically release eggs and sperm freely into the water, giving rise to a trochophore larval stage followed by a short (seldom longer than two or three days) planktotrophic veliger stage. Some acmaeids, trochids, fissurellids, and neritaceans deposit eggs in a gelatinous mass, from which pelagic veligers or benthic juveniles may emerge.

Mesogastropods and neogastropods exhibit internal fertilization, with oviparous or ovoviviparous development. Young may emerge as planktotrophic pelagic veligers, lecithotrophic pelagic veligers, or crawling juveniles. The mesogastropods are developmentally the most plastic order of prosobranchs, and larval types may vary within a single superfamily, family, genus, and in a few reported cases, a single species. The intriguing phenomenon of intraspecific variation in developmental types, reviewed by Robertson (1974; see also Spight 1975) is best documented in the Vermetidae (Hadfield et al. 1972).

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[5] Note that the converse is often not the case; protoconch morphology can only occasionally form the sole basis for distinguishing supraspecific taxa (Dall 1924; Smith 1945, 1946; Robertson 1974; Marshall 1978). Despite this limitation, certain authors, such as Iredale (1910, 1911), Grabau (1912), and Finlay (1931) have considered protoconch morphologies to be highly reliable characters, and some genera and subgenera are still differentiated exclusively on the basis of protoconch differences.

On closer scrutiny, many supposed examples of intraspecific variation have proven to be due to unrecognized cryptic or sibling species [e.g. the polychaete *Capitella capitella*, see Grassle and Grassle (1976, 1977); *Littorina saxatilis*, see Heller (1975); *Rissoa membranacea*, see Rehfeldt (1968) and Robertson (1974); *Calyptraea dilatata*, see Gallardo (1977a, b)].

The Littorinidae include nonpelagic as well as feeding and non-feeding pelagic larvae (Mileikovsky 1975; pelagic egg capsules which give rise to free-swimming veligers are present in many species, e.g. Bandel 1974). The Cerithiacea (Houbrick 1973), Calyptraeacea (Hoagland 1977), Cypraeacea (Ranson 1967; Taylor 1975), and Tonnacea (Taylor 1975) include a variety of development types as well. Among the more conservative groups are the Strombacaea, which are all reportedly oviparous with pelagic larvae; and the Rissoacea, which all follow one of two developmental pathways: those which hatch as crawling juveniles from relatively large eggs (140-320 μm, and those which hatch from relatively small eggs (60-130 μm) and spend 2-3 weeks as planktotrophic veligers (Taylor 1975).

Some mesogastropods have an unusual larval form known as the echinospira larvae, in which an outer transparent shell or membrane (scaphoconch) is developed in addition to the calcified shell, with the space between the two filled with sea water. Fretter and Graham (1962) have suggested that the outer "shell" is actually of proteinaceous, periostracal origin. This flotation aid, lost at metamorphosis, is reported in the Eratoidae, Lamellariidae, Capulidae (Lebour 1935, 1937; Fretter and Graham 1962), Trichotropidae (Pilkington 1974), and the Hipponicidae [Cernohorsky 1968; Robertson (1974, p. 221) states that this observation requires confirmation].

The neogastropods, an ecologically more homogeneous group, show a greater uniformity in mode of development. Among the "stenoglossan" neogastropods (Muricacea, Volutacea, Buccinacea), oviparous development predominates and culminates in a crawling juvenile stage.[6] This mode of development generally involves deposition of large eggs (400-600 μm) in capsules attached to hard substrata. Pelagic larvae are known, however, from all three superfamilies (Scheltema 1971; Radwin and Chamberlin 1973; Taylor 1975; Bandel 1976b; Spight 1976b, 1977). Marche-Marchad (1968) describes an unusual case of ovoviviparity in the volutid *Cymbium* ("*Cymba*") which retains its egg capsules within an enlarged pedal gland. The toxoglossan neogastropods (Mitracea and Conacea) appear to have a higher proportion of pelagic larvae than do the stenoglossans.

Little information is available on the larval ecology of opisthobranchs. Here we will deal only with taxa most likely to have a good fossil record; for more extensive recent reviews, see Beeman (1977) and Bonar (1978). The most primitive group, the Order Heterogastropoda (Architectonicacea, including Mathildidae and Architectonicidae; Triphoroidea; Epitoniacea; Pyramidellacea;

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[6] 70% of the 170 species listed by Radwin and Chamberlin (1973) exhibited this mode of development.

see Kosuge 1966; Climo 1975; Marshall 1977a, b).[7] Shelled ospithobranchs generally have heterostrophic protoconchs--the protoconch is sinistrally coiled, in the opposite direction to the dextral teleoconch. Architectonicaceans have planktotrophic larvae that can remain in the plankton for, in some cases, well over three months (Robertson 1964; Robertson et al. 1970); eggs are as small as 63 μm, with settling individuals attaining sizes in excess of 3-6 Protoconch II whorls before metamorphosis (Taylor 1975). Little is known of triphorid development; of the 27 species of *Triphora* reported from Hawaii, all species (with one possible exception) apparently have a pelagic veliger stage (Taylor 1975). Marshall (1977a, b) provides scanning electron micrographs of triphorid protoconchs. For the Pyramidellacea, Rodriguez Babio and Thiriot-Quiévreux (1975) describe four types of pyramidellid protoconchs, two of which are apparently associated with planktotrophic development, and two in which the pelagic phase is brief or absent.

For the Cephalaspidea, various authors report planktotrophic development (*Philine* spp., Brown 1934; Horikoski 1967; *Acteocina canaliculata*, Franz 1971), lecithotrophic development (*Haloa japonica*, Usuki 1966), true direct development (*Runcina* spp., *Acteocina senestra*; see references in Baba and Hamatani 1959; Bonar 1978), and *in capsulo* veliger development, with crawl-away young (*Retusa obtusa*, Smith 1967).

The development of marine pulmonates (belonging to the lower Basommatophora) has been reviewed by Berry (1977). Most siphonariids hatch as planktotrophic veligers, while the remaining families (Ellobiidae, Otinidae, Amphinolidae, Chilinidae), for the most part, exhibit nonpelagic development, emerging from egg capsules as crawling juveniles. As in the case of the opisthobranchs, there is a general tendency for protoconchs to be heterostrophic.

Bivalvia

Terminology. Bivalve larval shell terminology as employed herein is analogous to that for gastropods, and is generally compatible with the terminology of Werner (1939), Rees (1950), Ockelmann (1965), and Cox (1969). The *prodissoconch* is the entire shell formed prior to metamorphosis and is considered in this chapter to be synonymous with the term "larval shell." *Prodissoconch I* is the first shelled stage developing from the non-shelled trochophore, and is secreted by the shell gland and mantle epithelium (Carriker and Palmer 1979). Prodissoconch I tends to have a granulated appearance under the optical microscope, which resolves into a coarse and irregular punctate surface texture under the SEM. This stage is equivalent to Werner's (1939) special usage of the term *veliger*,[8] which has been followed by many European workers, and to the protostracum of Bernard (1898). On the basis of shape, this stage is also known as the D-shaped or straight-hinged veliger. The straight-hinge stage, however, does not exactly coincide with the Prodissoconch I stage and is considered to persist until total shell length is twice the length of the hinge-line (Chanley and Andrews 1971).

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[7] Some or all of these taxa may actually be prosobranchs, and the Heterogastropoda may, in fact, constitute an artificial group.

[8] In this chapter, the term veliger refers to a shelled molluscan larva which possesses a velum (ciliated swimming organ), an adaptation for a free-swimming existence. This velum is lost or resorbed at the time of final settlement and

Prodissoconch II is deposited by the mantle edge along the shell margins and inside the Prodissoconch I valves (Carriker and Palmer 1979). At this stage, the larva is referred to as a veliconcha by Werner (1939) and subsequent European workers. The thickened hinge region of the shell, which may support an interlocking tooth system, is termed the provinculum (Bernard 1889). Prodissoconch II shows concentric growth lines, and sometimes exhibits other ornamentation as well (LaBarbera 1974). However, the great diversity of surface features seen in gastropods at the protoconch stage is not present in the bivalve prodissoconch. The term pediveliger (Carriker 1961) has been applied to a late larval stage marked by the coexistence of a velum and a "foot" that has undergone rapid growth "in preparation for" a benthic existence (Fig. 2B).

The dissoconch constitutes the shell deposited after metamorphosis. Ornamentation, surface texture, and parameters of dissoconch shell growth may contrast markedly with the prodissoconch (Fig. 8). A sharp transitional line of demarcation, the metamorphic line, is often clearly evident at the Prodissoconch II/dissoconch boundary (Carriker and Palmer 1979).

In bivalve larvae, the provinculum and larval shell commissure provide a datum for a standard plane of reference. Shell dimension terminology followed in this chapter is diagrammatically illustrated in Figure 9. Length is the greatest shell distance measured parallel to the hinge line. Height is the greatest shell distance in the dorso-ventral (commissural) plane perpendicular to the length (= width of some authors). Depth is the maximum distance through the larva from right to left valves, perpendicular to the larval commissure; this dimension has variously been called thickness, convexity, and width, by other authors. These and other morphologic terms are defined in a glossary prepared by Chanley and Andrews (1971).

Criteria. As with gastropods, the key character in separating planktotrophs and nonplanktotrophs is the initial calcified growth stage, Prodissoconch I. The Prodissoconch I of species having planktotrophic larvae is relatively small (70-150 μm in length), reflecting the low yolk supply of the egg (Ockelmann 1965). Prodissoconch II, deposited during the veliger stage, is large (200-600 μm in length) relative to Prodissoconch I. The Prodissoconch II stage of species with planktotrophic larvae is generally devoid of surface ornamentation except for growth lines (Fig. 10A). Species with lecithotrophic pelagic larvae generally have a relatively large Prodissoconch I (135-230 μm, depending on the species; Ockelmann 1965). A distinct

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metamorphosis. Certain species which undergo development through metamorphosis entirely within the confines of an egg capsule nevertheless pass through a veliger stage.

Prodissoconch II interposed between Prodissoconch I and the dissoconch is relatively small or absent (Fig. 10B). This probably reflects the short time lecithotrophs spend in the plankton, although a direct relationship between planktic duration and Prodissoconch II size has not been quantitatively demonstrated. Species with larvae which have no pelagic stage (e.g. certain brooded larvae) have the largest eggs of all, producing a Prodissoconch I of 230 to over 500 µm in length. The Prodissoconch I of such larvae is often inflated, lacking the distinctive D-shape (see Ockelmann 1965; Chanley and Andrews 1971; LaBarbera 1974) and may show irregular folds and wrinkles. While many nonpelagic larvae are brooded within the parent's gill lamellae or pallial sinus, some nonpelagic species undergo development outside the parent. For example, *Musculus discors* and *M. niger* release egg strings into a byssal nest, from which young hatch as crawling juveniles (Thorson 1935). Ockelmann (1965) suggests that the encapsulated eggs released by certain *Astarte* also hatch as benthic juveniles; a similar mode of development is reported by Blacknell and Ansell (1974) for the lucinacean *Thyasira gouldi*. The latter authors provide an excellent brief review of the distribution of lecithotrophic development in the Bivalvia.

While the above criteria provide useful guidelines, it should be mentioned that interpretations based on egg and Prodissoconch I size are sometimes ambiguous. For example, Allen and Sanders (1973) report that, while egg size in certain deep-sea Nuculanacea indicates a borderline planktotrophic or lecithotrophic mode of development, Prodissoconch I size indicates nonpelagic or lecithotrophic development. As with gastropods, the most reliable means of inferring developmental type from prodissoconch morphology is through comparison with confamilial or congeneric species for which the development is known (e.g. LaBarbera 1974).

Identification of larval shells is facilitated by examination of the provinculum and associated lateral hinge system (Fig. 11). Denticulated structures associated with the provinculum are diagnostic at the familial or superfamilial level, although they have no direct relationship to the dentition which develops in the adult hinge (Rees 1950, and numerous subsequent authors). Larval dentition is obscured shortly after metamorphosis by intraumbonal dissoconch growth. Rees (1950) provides diagrammatic figures (see Fig. 12) of the hinge apparatus of most of the North Sea bivalve superfamilies having pelagic larvae (see Guérin 1973, for useful discussion); the Pectinacea and Anomiacea were found to share a single larval hinge type, as were the Pteriacea and Ostreacea. Rees (1950) recognizes five major provinculum types (Table 1):

a. Several or numerous rectangular teeth or crenulations in a row along a relatively thick provinculum, reminiscent of adult arcoid taxodont dentition (found in larval Mytilacea, Pectinacea, Anomiacea, Pteriacea, Ostreacea, some Veneracea, some Mactracea, and Tellinacea).

b. One, two or three strong rectangular teeth in each valve arranged along a relatively thick provinculum (Astartacea, some Cardiacea, some Solenacea, Hiatellacea, Myidae and some Corbulidae and Pholadacea).

c. A few teeth on a relatively thin provinculum (some Cardiacea, some

Mactracea, Pandoracea and Poromyacea).

d. Right valve has spiky teeth (on a thin strip) that insert into sockets on the left valve (some Cardiacea, some Solenacea, and some Corbulidae).

e. A thin provinculum from which teeth are entirely lacking (Lucinacea and Erycinacea).

In his studies, Rees (1950) relied on optical microscopy; however, structural details of the larval hinge apparatus are more readily discerned using scanning electron microscopy (Fig. 13).

A further aid to identification of larval shells is the configuration of the lateral hinge system (Rees 1950; see also Cox 1969), situated on the dorsal shell margin anterior and/or posterior to the provinculum (Fig. 11). A projecting flange, when present, is generally on the left valve, interlocking with the right valve between the dorsal margin of the shell and an internal ridge. Near the junction of this ridge with the provinculum there may be a "lamellar" or "solid" tooth-like projection (Rees 1950). Lamellar lateral teeth are thin and elongate, and interlock with a groove bordered by the rim of the opposite valve. Solid lateral teeth are more massive than lamellar lateral teeth and, unlike the latter, come into contact with the outside edge of the provinculum of the other valve when the shell is closed. There are also large special teeth that cannot be readily considered as part of either the provincular or lateral hinge systems (Rees 1950). These larger projections are located at the juncture between the two hinge systems and exhibit various shapes; Rees reports them from the Astartacea, Mactracea, Tellinacea, and Poromyacea. Chanley (1969) has suggested that in the Tellinacea the "special teeth" belong to the structure of the juvenile post-settlement hinge, and do not appear until late larval life or after metamorphosis. A much closer scrutiny of larval hinge features, as well as soft part morphology, is possible with the scanning electron microscope (e.g. Scheltema 1971b; Culliney and Turner 1975; Turner and Boyle 1975; LaBarbera 1975; Lutz and Jablonski 1978b), and may be used to distinguish larvae to genera and species (e.g. Booth 1977; Lutz and Jablonski 1978c; Lutz 1977, 1978; Lutz and Hidu 1979).

Shell shape is also important in taxonomic placement of larval shells (Werner 1939; Rees 1950; Yoshida 1953; Miyasaki 1962). Relative prominence of the umbo (in the Prodissoconch II stage) and height/length and length/depth ratios are particularly useful. Chanley and Andrews (1971) provide a glossary and numerous examples of species-level separation on the basis of shape (see also Loosanoff et al. 1966).

The presence and position of ligaments or "ligament pits" ("possettes ligamentaires") has been considered another diagnostic characteristic useful in superfamilial separation of larval specimens (Bernard 1896; Rees 1950; Ansell 1963; Loosanoff et al. 1966; Chanley and Andrews 1971; LePennec and Masson 1976; Bayne 1976). The designation of many of these structures as larval features may be misleading, if not entirely inappropriate (Lutz 1977, 1978; Lutz and Jablonski 1979; Lutz and Hidu 1979). Lutz and Hidu (1979), in their study of hinge morphogenesis of larval and early post-larval bivalves, suggested that ligament attachment sites are not visible, using either optical or scanning electron microscopy, until larvae are at least "capable of metamophosis," and concluded that "many of the morphological features heretofore interpreted in optical micrographs as larval ligaments are actually post-larval ligament pits." The aragonitic fibrillar structure of such ligament pits may be responsible for the optical density differences observed in published micrographs.

Taxonomic distribution. About 60-75% of shallow-water marine bivalves have planktotrophic larvae. Other developmental types are apparently more dependent on latitude and other ecologic factors than on taxonomic relationships, with confamilial or congeneric species sometimes exhibiting very different developmental histories. References given in this section are intended only to provide recent information on larval types, and an entry into the literature; for older compendia see Lebour (1938), Thorson (1946), Sullivan (1948), Ockelmann (1958), Loosanoff and Davis (1963), Loosanoff et al. (1966).

The protobranchs, which include the Orders Nuculoida, Nuculanoida, and Solemyoida (Allen 1978), exhibit an unusual (primitive? Chanley 1968) mode of development (Fig. 14A, B). Larvae develop from large eggs and are lecithotropic, with development often taking place within a free-swimming ciliated test that is cast off at metamorphosis after a short pelagic existence [Drew 1899, 1901; Chanley 1968; nonpelagic species are also known, see Scheltema (1972)]. Development within the arcoids (Chanley 1966; Tanaka 1971), mytiloids (Chanley 1970; Ockelmann 1965; Bayne 1976; Booth 1977), and pterioids (Tanaka 1970; Ota 1961) is generally by means of the more familiar planktotrophic veliger larva, with some lecithotrophic and a few nonpelagic larval types known in each order. Among the ostreoids (Waller 1978), the scallops also are dominantly planktotrophic (Sastry 1965; LePennec 1974; Culliney 1974), while the oysters show a tendency toward mantle cavity brooding, generally accompanied by lecithotrophy. The brooding habit is present in *Ostrea*, *Alectryonella*, and *Lopha*, while *Crassostrea*, *Saccostrea*, and *Striostrea* are known to be non-brooding (Stenzel 1971). In the veneroids, the Lucinacea (Blackness and Ansell 1974), Galeommatacea, (Chanley and Chanley 1970; Franz 1973), Cyamiacea, Carditacea (Jones 1963; Yonge 1969), and Crassatellacea (Harry 1966) show a tendency toward lecithotrophy and ovoviviparity, while the Cardacea (Kingston 1974a, b), Tridacnacea (LaBarbera 1975; Jameson 1976), Macracea (Chanley 1965), Solenacea, Tellinacea (Chanley 1969) Arcticacea (Landers 1976), and Veneracea (LaBarbera and Chanley 1970; LePennec 1973) are predominantly planktotrophic. The Myoida also are primarily planktotrophic in their development (Boyle and Turner 1976; Chanley 1965; Culliney 1975; Culliney and Turner 1976). For the Pholadomyoida, Chanley (1968; Chanley and Castagna 1966) states that the Pandoracea are lecithotrophic [although Ockelmann (1965) figures a planktotrophic species of *Thracia*]. The hinge-line of pandoracean larvae is slightly indented; consequently, the straight-hinge stage is absent (Fig. 14C). The few species of Poromyacea which have been studied have lecithotrophic larvae (Ockelmann 1965).

IV. ECOLOGICAL AND PALEONTOLOGICAL APPLICATIONS

The distribution of larval types is clearly nonrandom in space and time, although we have yet to gain complete insight into the controlling factors. Furthermore, the evolutionary impact of different developmental histories is just beginning to be explored. Here, we will briefly discuss a few areas of research in which studies of larval ecology and paleoecology could make a significant contribution.

Ecological Applications

Adaptive and developmental strategies. Phylogenetic relationships appear to be of secondary importance in determining developmental type in marine benthos. At first glance, the distribution of larval types appears to conform to the predictions of the r-K model for reproductive strategies [MacArthur and Wilson 1967; Pianka 1970; Gadgil and Bossert 1970; Gadgil and Solbrig 1972; Southwood 1976; see Stearn (1976, 1977) for a discussion and critique]. In shallow marine waters, the more generalized, "opportunistic" species (supposedly "r-strategists") have a high rate of gamete production, and produce small planktotrophic larvae which receive little or no parental care; populations may show wide annual fluctuations (Thorson 1950, 1966; Coe 1953, 1956). The more specialized, "equilibrium" species (supposed "K-strategists") produce fewer, larger eggs, invest more energy reserves per offspring, and have nonplanktotrophic larvae; Mileikovsky (1971) cites evidence that these species tend to have more stable populations. This mode could be invoked, for example, as an explanation for the presence of planktotrophic larvae in the opportunistic bivalve *Mulinia lateralis* (Calabrese 1969, 1970; Calabrese and Rhodes 1974), and pelagic lecithotrophic or nonpelagic larvae in *Nucula* and other protobranchs which are seemingly more K-selected (Rhoads et al. 1978). Similar reasoning could be followed in explaining the prevalence of nonpelagic larvae in the carnivorous neogastropods, which are at a high trophic level and may be more specialized than many of the archeogastropod and mesogastropod groups that have pelagic larvae (cf. Radwin and Chamberlin 1973; Shuto 1974). When habitats or trophic resources are predictable or species are adapted to life within rather narrow environmental limits, survival of offspring is likely to be higher if larvae do not disperse any great distance from the parent [see Vermeij (1972) on tropical high intertidal gastropods, and Hadfield (1963) on nudibranch development as related to prey population structure]. That is, a good indication of the suitability of a habitat is the survival of individuals to reproductive age. On the other hand, Strathmann (1974) suggests that when the parent cannot "predict" whether its present location is likely to provide a better setting for survival and reproduction of its offspring than some other location, high dispersal is the optimal strategy. When prey species exhibit relatively small population fluctuations, as in the tropics and other "favorable" environments, predator species can rely more heavily on fewer, more localized prey populations (MacArthur 1972; Vermeij 1978). For recent discussions of life-history strategies in nonmarine bivalves and gastropods, respectively, see Heard (1977) and Calow (1978).

Another interesting trend is seen in the latitudinal distribution of developmental types shown in Figure 15. According to Thorson (1950, 1965), larvae of approximately 57-68% of the marine prosobranchs from Gibraltar to Trondheim on the Norwegian coast are pelagic (planktotrophic or lecithotrophic with a brief pelagic stage), while north of this point, the proportion of species with pelagic larvae declines until it reaches about 17% near Murmansk [see also Spight (1977) on the Muricacea]. Ockelmann (1965) reports a similar trend (sometimes called "Thorson's Rule"; Mileikovsky 1971) in the eastern Atlantic shelf Bivalvia, with about 75% of the Gibraltar bivalves having planktotrophic larvae (about 17% lecithotrophic with a short pelagic stage, and about 8% nonpelagic), while only 15% of the Spitsbergen bivalves have planktotrophic larvae (about 37% pelagic lecithotrophic, and 48% nonpelagic). Dell (1972) reports a similarly high incidence of viviparity and ovoviviparity in Antarctic benthos as well.[9]

The above observations stand in contrast to our first-approximation assignment of species with planktotrophic larvae to the r-selected end of the adaptive strategy spectrum, and species with nonplanktotrophic larvae to the K-selected end of the spectrum (see also Valentine and Ayala 1978).[10] The latitudinal pattern may be more consistent with the predictions of a stochastic mode for the evolution of life history strategies [e.g. Murphy 1968; Schaffer 1974; Stearns 1976 (the "bet-hedging model"), 1977]. This model suggests that where juvenile mortality fluctuates more than adult mortality, organisms with delayed reproduction, low reproductive efforts, and a few young are favored. Thus, for species or situations in which fluctuations in population densities result primarily from fluctuations in survival of early growth stages, evolution will lead to a complex of characteristics more typical of K-selection than of r-selection regimes. This may be the case in high latitude molluscs, where harsh conditions in surface waters (salinity fluctuations, short, intense seasonal bursts of phytoplankton production, low temperatures,[11] etc.) might lead to unusually high pelagic larvae mortality. Conversely, in situations where adult mortality fluctuates more than juvenile mortality, so-called r-selected traits would be expected. Thorson (1950) attributed this latitudinal pattern to the timing of primary production [for critique, see Menge (1975)]; phytoplankton blooms become progressively shorter in duration at high latitudes and thus time available to planktotrophic larvae for completion of growth and metamorphosis is progressively restricted. This problem would be compounded by the slower metabolic and developmental rates brought about by the colder water temperatures of high latitudes (e.g. Vermeij 1978).

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[9] Dell (1972) points out that this short or non-existent pelagic stage need not invariably lead to a limited geographic distribution. In Antarctic waters, at least, ovoviviparous species have often achieved the widest geographic distributions, and he attributes this to passive dispersal by attachment to floating algae (see also Arnaud 1974; Arnaud et al. 1976; Simpson 1977). Dell (1972, p. 163) stresses that the "significance of such a bivalve arriving in a new area with several hundred well-developed young ready for release is obvious enough." However, it seems unlikely that this could serve as a general mechanism for widespread dispersal of subtidal benthos.

[10] If one accepts that on the whole, density-independent physical factors are more important in temperate to polar waters, while density-dependent biological interactions predominate in tropical areas (Dobzhansky 1950; Sanders 1968; MacArthur 1972).

[11] Lower temperature might indirectly contribute to increased larval mortality by depressing developmental rates and thus prolonging the duration of exposure to predation while in the plankton (Vance 1973a).

Thorson's (1950) observation of an increase in the proportion of pelagic to nonpelagic larvae from temperate to equatorial waters (Fig. 15) may in part be an artifact of the faunas studied to that date (Radwin and Chamberlin 1973). Thorson's original data were obtained from the Persian Gulf (the waters of which are subject to unusually high temperatures and salinities), and oceanic islands (Bermuda, and the Canary Islands, in which initial colonization would likely have been limited to planktotrophic species). Unless mainland species were fortuitously transported to the isolated islands, say by rafting or human activities, the only nonpelagic developmental histories present would have to evolve *in situ*. The fact that any species with nonpelagic development are found on oceanic islands probably testifies to the intensity of selection favoring this developmental type. Curtailment of the pelagic phase could be an adaptation to avoid mass loss of larvae which might otherwise be carried by prevailing currents away from the islands and into the open ocean. This may explain why young oceanic islands, such as Ascension Island, tend to have a molluscan fauna with predominantly pelagic larvae (Rosewater 1975), while older islands have a higher proportion of species with nonpelagic larvae (cf. compilations of Thorson 1965; Radwin and Chamberlin 1973). The landward component of near-bottom coastal water movement may also play a role in preventing larvae from being lost to the open ocean (see Scheltema 1975).

A similar trend in reproductive types is seen in intertidal-subtidal transects (Jackson 1974), and from the subtidal shelf into the deep sea. Thorson (1950) predicted that deep-sea molluscs would dominantly show nonpelagic development with planktotrophic development being least common. More recent studies (Ockelmann 1965; Knudsen 1970; Scheltema 1972; Grassle and Sanders 1973; Sanders and Allen 1973, 1977) have shown that lecithotrophy (with a brief, nonfeeding pelagic stage) is the most common mode of development among deep-sea molluscs [78% of the 23 bivalve species examined by Knudsen (1970) had lecithotrophic development]. Planktotrophy appears to be rare among deep-sea molluscs, although it is apparently important in other deep-sea taxa [e.g. ophiuroids, Schoener (1968, 1972)]. Despite this low dispersal capability, the relatively broad distribution of deep-sea molluscs (Scheltema 1972; see also Allen 1979) suggests that this developmental strategy is a response to the long-term stability of the deep-sea habitat, and thus can again be linked to the K end of the r-K spectrum.[12] Dispersal could proceed in a stepwise fashion in a homogeneous environment over a long period of time. On the other hand, Bouchet (1976) has used the criteria discussed here to infer planktotrophic development from shell morphology of a number of deep-sea gastropods (Fig. 16). He considers planktotrophy to be an important factor in maintenance of genetic continuity among populations in deep basins separated by major bathymetric features (e.g. the mid-Atlantic ridge). Bouchet believes that these species have pelagic larvae, which rise to feed in the photic zone, but it is not obvious how the larval shells of planktotrophic pelagic species and demersal species might be distinguished. Both types of larvae are capable of feeding during development, and thus would be expected to each have a small Protoconch I. Pelagic or demersal larvae are also found in deep-sea molluscs that inhabit such rare, transient substrata as decomposing wood (pholadacean bivalves; Turner 1973).

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[12] Note that in a certain sense this reproductive pattern might be regarded as a taxonomic artifact, in that the protobranchs greatly dominate deep-sea bivalve collections (Allen 1971, 1978).

Also underlying the distribution of larval types in marine organisms is the relationship between body size and developmental strategy (which of course need not be mutually exclusive with the relationship between life history traits and development). Because of the great larval mortality associated with planktotrophy, species following this developmental mode must release immense numbers of larvae. As body size becomes small, so does the absolute amount of energy available for reproduction (Giesel 1976). Below a certain size, species will be unable to produce enough planktotrophic larvae to ensure survival of the population(s) because of the high mortality accompanying this mode of development. Here, the most efficient strategy is to invest a greater proportion of energy per offspring in a few eggs which have a relatively good chance of surviving to complete their development[13] (Mileikovsky 1971; Arnaud 1974; Chia 1974; Menge 1974, 1975; Simpson 1977; McCall 1977; Hoagland 1977; Gould 1977). For example, Sellmer (1967) presents a partial tabulation of known cases of brooding in bivalves, and, except for the oysters, all species have a very small body size. Thus, in the case of the geographic and depth-related patterns discussed above, the diminutive size of most deep-sea (Sanders and Allen 1973; Allen 1978) and high-latitude (Arnaud 1974; Nicol 1964, 1966, 1978) molluscs, which is presumably related to limited nutrient supply (Thiel 1975) and/or temperature-controlled growth rates (Gunter 1957) may govern the nature of their developmental histories. These species are "forced" to adopt a nonplanktotrophic strategy because they are unable to produce enough planktotrophic larvae per breeding episode to ensure adequate recruitment. Lack of a planktotrophic larvae in the deep sea [just as Thorson (1950) cited brief productivity episodes in high latitudes], but the ability of larvae to utilize detritus and dissolved nutrients cannot be ruled out (e.g. Pilkington and Fretter 1970).

It appears that competition (Menge 1974, 1975) and selective predation on larger-sized individuals (Brooks and Dodson 1965; Dodson 1970; Menge 1973) can also lead to an optimum reproductive size that requires nonplanktotrophy. Spight (1976b) further notes that large hatching size may aid in reducing predation and physiological stress among juveniles (see also Woodin 1976).

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[13] Although mortality of embryos in egg capsules is also not trivial, e.g. 42% in *Thais lamellosa* (Spight 1975).

This adaptive link between body size and mode of reproduction is probably also a primary factor in the discordance between reproductive strategies in marine benthos and the r-K model. Many of the most strongly opportunistic species in the marine realm have nonpelagic larvae (Grassle and Grassle 1974, 1977). Small adult size, and attendant rapid onset of reproductive age, are characteristics of these species, which in many cases compensate for low adult yield per reproductive episode by reproducing several times, with only brief intervening pauses (e.g. Grassle and Grassle 1974, 1977). This is in contrast to Pianka's (1970) generalization that r-selected species have a single reproductive episode per generation. Menge (1974, 1975) has suggested that this strategy occurs in the brooding starfish *Leptasterias hexactis*. Small body size is maintained by interactions with a superior competitor (*Pisaster ochraceus*, which is thus ostensibly the K-strategist of the pair) which releases large numbers of planktotrophic larvae. Grahame (1977) has attempted to reconcile these results with the r-K model by stressing the prediction (Gadgil and Solbrig 1972) that r-selected species will allocate a greater proportion of their energy reserves to reproduction. *L. hexactis* does invest more energy in reproduction than *P. ochraceus*, and by this criterion could be regarded as more r-selected, despite its low gamete production per reproductive episode. In two species of the littorinid snail *Lacuna*, Grahame (1977) found that the species exhibiting greater reproductive effort, and showing other r-selected characteristics as well, had long-lived planktotrophic larvae. However, it is premature to generalize on the relationship between mode of development and energy expenditure of the parent in marine organisms; no universal correlation emerges from the sparse literature.

In an evolutionary context, small body size might be readily attained by progenesis (acceleration of gonad maturation relative to somatic growth), a mechanism Gould (1977) links to an "r-selected" regime. This, in turn, would rule out planktotrophic larvae in the life histories of these species if a critical threshold was crossed below which insufficient numbers of planktotrophic larvae could be produced. For example, Gould (1977, pp. 327-328) has suggested progenesis for the origin of the assemblage of minute bivalves described by Soot-Ryen (1960) from Tristan de Cunha; Gould envisions this as a response to superabundant resources by a number of normal-size species that drifted in via planktotrophic larvae. Seven or eight of the tiny, progenetic descendants of the initial colonizers are brooders. Gould (1977) presents a number of other marine examples, along with a discussion of the ecological situations most conducive to progenesis, such as unstable environments, colonization, parasitism, and a variety of habitats favoring small size *per se*.

Consideration of the selective forces and adaptive responses acting here can lead to a chicken-egg paradox. We must caution that the inter-relationships among body size, adaptive strategy, dispersal capability, and environmental tolerance is a complex and fundamental one. It is difficult, and perhaps inappropriate, to single out any one factor in an attempt to explain the constellation of traits displayed by an assemblage of more or less disparate organisms. Clearly, a more precise understanding of the distribution of developmental types in all latitudes, depths, and colonization situations is desirable, and the link between development and larval shell morphology provides a relatively simple and direct way of accumulating the

the necessary data.

Environmental monitoring. The recolonization of a sea floor or intertidal zone following a natural or anthropogenic perturbation is likely to reflect dispersal capabilities of the affected species. Two interrelated phenomena will underlie this response: (1) the differential ability of a species to spread larvae into new areas or recolonize disturbed habitats; and (2) the imprecise, but direct correlation between dispersal capability and environmental tolerance. For example, following defaunation of a Florida intertidal zone by a red tide, two gastropod species which have nonpelagic larvae (*Nassarius vibex*[14] and *Prunum apicinum*) had not returned by 24 months after repopulation had begun (Simon and Dauer 1977). It appears, then, that examination of protoconch and prodissoconch morphology should allow environmental monitoring studies to:

(1) "Factor out" the effects on slow colonizers following a disturbance. That is, species with nonplanktotrophic larvae, and especially those with nonpelagic larvae (with the exception of certain extreme opportunists), could be predicted *not* to return in the early stages of recolonization. Negligible recovery of populations of species having planktotrophic larvae would be a better indicator of extensive or lasting damage to environmental quality than would a gradual return of species having low-dispersal larvae, and these two groups should be weighted accordingly in assessing and predicting recolonization sequences.

(2) Establish a cutoff point for recognizing "acceptable" pollution levels in regions in which there are temporal or spatial gradients in disturbance, such as point-source thermal or chemical effluents. A significant decline in the populations of species having nonplanktotrophic larvae will indicate that the community is becoming disturbed beyond its limits of resilience (see Rhoads et al. 1978), as repopulation by these components of the ecosystem will be a long and haphazard process (e.g. greater than 2 years in the case of the gastropods mentioned by Simon and Dauer 1977).

Paleontological Applications

Fossil shells sufficiently well preserved to be assigned with some confidence to the planktotrophic or nonplanktotrophic categories have been reported from Late Tertiary (e.g. Sorgenfrei 1958; LaBarbera 1974; Scheltema 1978, 1979a, b), Early Tertiary (Hansen 1978a, b), Late Cretaceous (Lutz and Jablonski 1978a, b, c; Jablonski 1978a, b, 1979; Jablonski and Lutz 1978), and even some Paleozoic deposits (Harrison 1978; J. Kríz, personal communication). Possible protoconchs have been described for an extinct class of Paleozoic molluscs (?), the Hyolitha (Ozik 1978). Application of the criteria outlined in this chapter to well-preserved fossil larval and early juvenile shells enables us to assess the effects of different developmental types from the unique time perspective of paleontology.

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[14] Possibly a misidentification; Scheltema (1962) describes pelagic larvae for this species.

Evolutionary patterns. Shuto (1974) and Scheltema (1977, 1978, 1979a, b) have developed models concerning the paleontological significance of differential dispersal capabilities. Planktotrophic species having a relatively long pelagic stage will have the ability to disperse over wide geographic areas in a single generation. Local catastrophes are unlikely to eliminate a species over its entire geographic range, and larvae from other, persistent populations will replenish populations reduced by local extinction. These effects will combine to produce a geologically long-lived species. Further, larval dispersal by ocean currents will maintain gene flow among disjunct populations of sedentary adults and thus suppress the genetic divergence required for allopatric speciation. There is some electrophoretic evidence for low levels of genetic differentiation among benthic species having pelagic larvae, relative to those having nonpelagic larvae (Berger 1973; Gooch et al. 1972; Snyder and Gooch 1973; reviewed in Gooch 1975; see also Wilkins et al. 1978; Campbell 1978). This pattern is, however, complicated by the effects of differential mortality in a heterogeneous environment (e.g. Struhsaker 1968; Koehn 1976; Koehn et al. 1976; Milkman and Koehn 1977; Marcus 1977; Levinton and Lassen 1978) and recent genetic bottlenecks (Berger 1977). Local intense natural selection may cause populations to diverge despite larval dispersal if propagules from distant populations do not survive to reproductive age.

Species having nonplanktotrophic larvae will tend to have smaller, necessarily more continuous geographic ranges. As a result of the more restricted geographical (and, often, ecological) range of species with nonplanktotrophic larvae, local catastrophes and random population fluctuations are more likely to result in the extinction of the species. Local populations will tend to remain isolated after initial colonization or separation from the parent population, and thus speciation will be more common among such groups.

The above predictions, and the observations from which they were derived, were made for situations in which major oceanic barriers are present. However, there is some evidence that the effects of differential dispersal capabilities are significant even along a single continental shelf or within an epicontinental sea. Hansen (1978a, b) found, in the Lower Tertiary volutid gastropods of the Gulf Coast, that species having "planktonic" larvae had a mean duration of 4.4 m.y., while those with "nonplanktonic" larvae had a mean duration of 2.2 m.y.; in addition, geographic range of "planktonic" species averaged about twice that of "nonplanktonics" (Fig. 17). Similarly, in a survey of Gulf and Atlantic Coastal Plain gastropods from the Late Cretaceous, Jablonski (1978a, 1979a) found that species having planktotrophic larvae had a mean duration of about 6 m.y., while nonplanktotrophic species had a mean duration of only about 3 m.y. In both studies, degree of environmental tolerance also played an important role in determining species longevity and geologic range (cf. Jackson 1974, 1977). This factor may be responsible for the lack of a simple direct relationship between planktotrophy and species longevity in Late Cretaceous bivalves (Jablonski 1978a).

Scheltema (1978) has elaborated on his earlier (1977) conceptual model by suggesting that lineages or clades having planktotrophic larvae will produce new species via "punctuated equilibria" (Eldredge and Gould 1972, 1977; Gould and Eldredge 1977; Stanley 1975a, 1978), by occasional isolation of small outlying populations which, once isolated, would tend to evolve rapidly into new species. Barriers which might disrupt the flow of larvae among marine populations are not easily envisioned. Sympatric and parapatric speciation processes (e.g. Endler 1977; White 1978; Rosenzweig 1978) would, of course, not require physical barrier formation and may play an important role in the multiplication of marine species. Nonetheless, Murphy (1978) has suggested a climatic isolating mechanism for allopatric speciation in the acmaeid limpet Collisella. During warming trends, planktotrophic larvae of a warm-water species will successfully settle at higher latitudes, thus extending the species' range. Subsequent cooling intervals will cause geographic ranges to contract equatorward again, but some populations might become isolated in suitably warm, higher latitude embayments. Should this isolation last long enough, speciation will occur (Murphy 1978). Threshold effects may also allow for rapid speciation near the edges of species' ranges along environmental gradients (Dodson and Hallam 1977).

Scheltema (1978) further suggests that species with nonplanktotrophic larvae would be expected to undergo a gradual transformation into new species because populations are more localized and genetically more homogeneous; thus, they will be particularly susceptible to selection pressures generated by environmental changes. However, good cases of gradualism may be rare even among species with nonplanktotrophic larvae; species are more likely to become extinct or migrate along with their shifting habitat or temperature regime than evolve in situ along with changing environmental conditions. Note also that if the parent population is small enough, evolutionary change in this lineage could be so rapid and localized as to be indistinguishable from punctuated equilibria in the fossil record. Schopf and Dutton (1976) present possible evidence in favor of phyletic gradualism in bryozoans having low dispersal capability, but the link between clinal geographic variation and speciation is still unclear (e.g. Gould and Johnston 1972; Endler 1977).

Evolutionary patterns in the fossil record will be affected by the bathymetric gradient in adaptive types discussed by Jackson (1974, 1977). Jablonski (1978b, 1979a) found evidence in Late Cretaceous coastal plain sediments that very nearshore fossil assemblages will tend to comprise species with greater geologic and geographic ranges (the latter, presumably a reflection of greater environmental tolerance), and will have a greater proportion of species with planktotrophic larvae, than deeper-water assemblages. Thus, although the more offshore assemblages inhabit a somewhat less heterogeneous habitat, low dispersal and relative stenotopy may combine to make speciation more likely in these molluscs than in those inhabiting very shallow water. This may be a more satisfying reconciliation between an allopatric model for speciation (Mayr 1963, 1970; Bush 1975; White 1978) and the observation that offshore assemblages are more diverse and less persistent than very nearshore ones (Bretsky and Lorenz 1970a, b; Bambach 1977) than Eldredge's (1974) suggestion that new species arise onshore and migrate to the offshore areas.

With larval shell morphology giving an indication of dispersal capability, it will be possible to better separate the processes underlying extinction and speciation (Scheltema 1978; Jablonski 1979a). Numerous authors (e.g. Moore 1954, 1955; Kauffman 1972, 1977a, 1978) have considered environmental stress to be responsible for both the extinction and origination components of species turnover rates. However, as Eldredge and Gould (1977, p. 36; see also Eldredge 1974; Bush 1975) point out, "directions and intensities have never been directly correlated with speciation rates." If speciation proceeds primarily via the formation of peripheral isolates (allopatry), rates through time will depend on species' ability to maintain genetic continuity among populations, i.e. on their dispersal capability. Thus, lineages having planktotrophic larvae should have lower speciation rates than taxa having nonplanktotrophic larvae.[15] An asymmetrical pattern of speciation rates through a transgressive-regressive cycle (e.g. Kauffman 1972, 1977a) can be expected only if transgressive-regressive cycles are asymmetrical with regard to degree of spatial heterogeneity on the affected shelf, which may, in fact, be the case.

We agree with Kauffman (1977a) and others (e.g. More 1954, 1955) that increasing environmental stress during regression will result in increasing extinction rates. Here, too, this effect will be ameliorated for species having planktotrophic larvae (see Jablonski 1979a). While extinctions within a single basin may be most closely correlated with degree of environmental tolerance as modelled by Kauffman (1977a), planktotrophic taxa will be more widespread and undergo a high proportion of local, rather than complete, exterminations. With the subsequent transgression, the same species (or a closely related descendant) can return to colonize the area. Nonplanktotrophic species will tend to be driven into extinction during regression (or any other major environmental perturbation), and lineages will often terminate. With the return of suitable habitats, recolonizing species will be derived from more distantly related stocks.

Biostratigraphy and Paleobiogeography. Kauffman (1975) has stressed that benthic species with pelagic larvae can spread over very wide geographic ranges instantaneously (in geologic terms), and thus will make good biostratigraphic index fossils despite the sedentary habit of the adults. For example, the Cretaceous inoceramid bivalves are reportedly more useful for correlating sediments in different paleobiogeographic regions than such classic pelagic index fossils as the ammonites and planktic foraminifera (Kauffman 1977b). The extensive geographic distribution of the inoceramids and certain other benthic species is probably due in large part to the presence of a pelagic larval stage (Kauffman 1975, 1977b; Theide and Dinkelmann 1977), although passive dispersal of adults attached to floating material cannot be entirely ruled out.

Application of the criteria discussed above will enable the biostratigrapher to choose groups within a fauna which are likely to be the most useful in interprovincial and intercontinental correlations by recognizing those taxa with planktotrophic, and especially teleplanic, larvae. Thus, artificially differentiated faunas, saddled with provincial systematics, need not be entirely restudied before improved correlations can be made. Perhaps most significantly, larval ecologic studies will shed some light on the processes underlying the different stratigraphic and geographic distributions already abundantly documented by biostratigraphers.

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[15] Again, this will not be completely exclusive of a eurytopy-stenotopy effect, as eurytopy and planktotrophy often co-occur in the same species.

Herein lies a paradox, commented on by Scheltema (1977), Jackson (1977), Kauffman (1977b), and others. Benthic species tolerant enough, and having larvae with a sufficient pelagic duration, to maintain a broad geographic distribution would not be expected to evolve very rapidly, in terms of either speciation or extinction rates. Yet valuable index species, including the inoceramids, must be sufficiently short-lived to enable the biostratigrapher to finely subdivide the stratigraphic succession. Some other aspects of the adaptive strategy [perhaps related to trophic level and/or life position (e.g. Levinton 1974; Kauffman 1977a, 1978)] must play a key role in keeping certain widespread lineages vulnerable to high extinction rates.

Recognition of differential dispersal capability can provide considerable insight into the processes underlying the geographic affinities of species assemblages as well as individual species. Partitioning of planktotrophic and nonplanktotrophic faunal components will allow paleogeographers to more precisely recognize the timing and nature of zoogeographic barrier formation between regions. For example, Shuto (1974) found that the number of nonplanktotrophic species shared among local faunas in the Philippine-Indonesian region markedly declines from the Late Miocene through the Pliocene and into the Early Pleistocene, while the percentage of shared planktotrophic species remains virtually constant. He infers that the Celebes Sea was forming during this interval, presenting a bathymetric barrier to the species with low dispersal capability, but was not wide enough to disrupt gene flow among populations of species with planktotrophic larvae.

Paleocommunity Studies. The population dynamics of ancient communities have only recently received much attention (e.g. Levinton and Bambach 1970, 1975; Richards and Bambach 1975; Walker and Alberstadt 1975; Walker and Parker 1976; Peterson 1977). Study of larval shell morphology in fossil assemblages will provide insight into some of the long-term ecological and evolutionary processes underlying the establishment, maintenance, and alteration of marine biotic associations. Estimation of proportions of developmental types through time (both in terms of numbers of individuals and species) will allow the paleoecologists to make an assessment of processes of recruitment, dispersion, and adult reproductive effort. Faunal composition of small size classes, as compared to adult size classes, may be interesting from the viewpoint of failed recruitment episodes, particularly since the presence of a ligament pit may enable the investigator to differentiate metamorphosed juveniles from pelagic larval shells (Lutz 1977, 1978; Lutz and Hidu 1979). By analogy with present-day forms, the presence of species with nonplanktotrophic larvae within more than one fossil assemblage may indicate relative spatial homogeneity on the sea floor, while species with planktotrophic larvae, as a result of both high dispersal and accompanying eurytopy, could be expected to be present in a wider spectrum of assemblages. Similarly, examination of larval types within richly fossiliferous horizons or shell concentrations should give insights into the mode of recruitment of the constituent populations. Among the molluscs (if not the polychaetes), species with nonplanktotrophic larvae will have small population sizes, low turnover rates, and will tend to be stenotopic. They are more likely to constitute a significant portion of fossil assemblages when the deposits have been accumulating over ecologically long periods of time under relatively constant conditions; mass mortalities involving single spatfalls will infrequently involve large populations of species with planktotrophic larvae. Stratigraphic condensation could be responsible for compressing this time span into an apparent single event-horizon (e.g. Fürsich 1978).

Paleoclimatology. Lutz and Jablonski (1978b) recently suggested that the morphometry of the bivalve Prodissoconch II could be used as a relative, and in some cases absolute, paleotemperature indicator. Of all the factors influencing the duration of delay of metamorphosis in modern bivalves, temperature appears to play the single most important role (e.g. Bayne 1965, 1971). For the few species which have been examined in detail, strong negative correlations have been found between temperature and maximum-larval shell size at metamorphosis (Bayne 1965; Sullivan 1948; Savage and Goldberg 1976). Figure 18 illustrates this relationship for living *Mya arenaria*. Maximum reported size at metamorphosis of *M. arenaria* cultured at 19-24°C was 228 μm (Loosanoff and Davis 1963), while a maximum of 310 μm was found at lower culture temperatures fluctuating between 16 and 19°C (Savage and Goldberg 1976). Similar temperature-settlement size relationships have been found in several mytilids (Bayne 1965; Siddall 1978), and in the oyster *Crassostrea virginica* (Carriker 1951, p. 24). At high temperatures, the high rate of growth may be insufficient to compensate for the short time available for feeding (due to temperature-accelerated developmental rates), and this results in a smaller maximum size at higher temperatures (Bayne 1965).[16]

Data concerning maximum size at metamorphosis are available in fossil material in the form of the prodissoconch-dissoconch boundary (Lutz and Jablonski 1978b). Variations in the maximum size (and perhaps mean size, although adequate Recent data are not yet available) of the prodissoconch within a species should largely be a function of temperature. Empirical observations reviewed by Lutz and Jablonski (1978b) indicate that, while such factors as individual genetic differences, food availability, and salinity will contribute to variation in larval size at metamorphosis, they will not mask the temperature effect.

Prodissoconch-dissoconch boundaries of specimens in sediments as old as the Late Cretaceous are readily distinguished (e.g. Fig. 10), and, when combined with size distribution data for larval specimens can be used to reconstruct relative and absolute temperatures:

(1) *Relative temperatures*. Detailed examination of changes in prodissoconch dimensions in a species through time at a single locality, or in a

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[16] This apparent temperature-mediated decoupling of rates of somatic growth and ontogenetic change (cf. Gould 1977) is of considerable interest in a group of organisms in which paedomorphosis has played a significant evolutionary role (Stanley 1975b).

series of localities along a single horizon, should provide an indication of temporal or spatial gradients for any interval containing adequately preserved faunas. Such paleotemperature gradient reconstructions should serve as an independent test of data derived from other shelled microfossils or stable isotope analyses. They will also be useful in nearshore deposits, where holoplanktic paleoclimatic indicators may be rare.

(2) Absolute temperatures. The long geologic duration of most bivalve species (Stanley 1977) suggests that absolute paleotemperature estimates might be achieved for Holocene, Pleistocene, and Pliocene environments using regressions of prodissoconch length on temperature for a variety of extant species. However, as with other quantitative paleoclimatic techniques (Imbrie and Kipp 1971; CLIMAP Project Members 1976; Sachs et al. 1977), the assumption of evolutionary stasis within species with regard to physiological processes may not be entirely warranted, and should be used with caution.

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ACKNOWLEDGMENTS

We thank the following for critical review of the manuscript and helpful discussions: Robert Robertson, Ruth D. Turner, Stan Rachootin, Richard R. Strathmann, Earl D. McCoy, Thomas R. Waller, Karl M. Waage, Donald C. Rhoads and Susan M. Kidwell. We are especially grateful to Rudolf and Amelie Scheltema for their hospitality and thorough review and comments, which significantly improved this chapter. T. R. Waller, C. Thiriot-Quiévreux and R. D. Turner generously provided some of their excellent scanning electron micrographs. Maxine Lane, Susan Shiminski and Betsy Dabakis kindly typed the manuscript. Supported in part by NSF grant EAR78-15536, EPA grant R804-909-010, and NOAA Sea Grant 04-7-158-44034.

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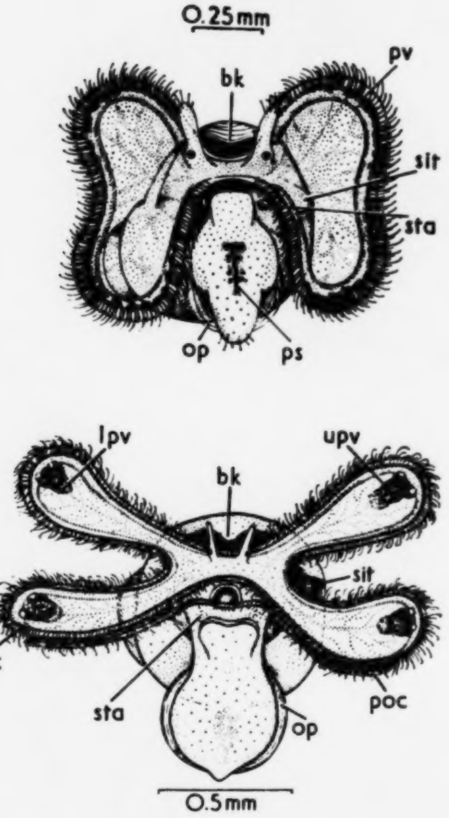

Figure 1. Gastropod veliger larvae. Above, Nassarius reticulatus, about 40 days old. Below, Nassarius incrassatus, swimming-crawling stage. Note interspecific differences such as pigmentation and velar lobe morphology. bk, beak of shell; f, foot; lpv, lower pigment patch of velum; op, operculum; poc, post-oral cilia of velum; prc, preoral ciliar of velum; ps, pigment on sole of foot; pv, pigment of velum; sit, siphonal tube; sta, staocyst; upv, upper pigment patch of velum. Reprinted with permission from Fretter and Graham (1962).

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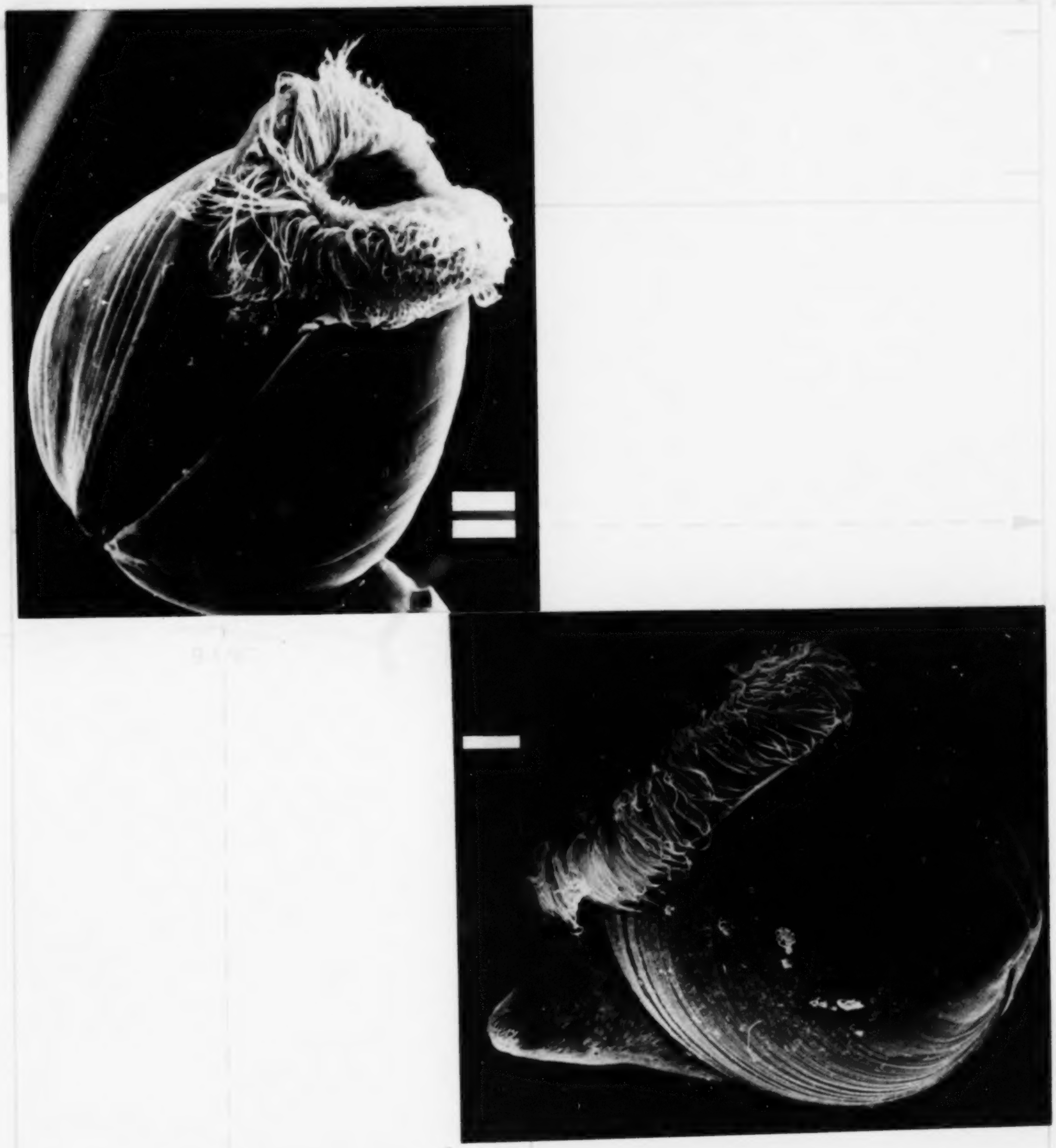

Figure 2. Critical-point dried bivalve larvae. (A) Veliger of *Ostrea edulis* (Ostreidae), 15 days after fertilization. Scale bar = 40 µm. Reprinted with permission from Waller (in press); scanning electron micrograph courtesy of Thomas R. Waller. (B) Pediveliger larva of *Lyrodus pedicellatus* (Teredinidae) showing extended foot and velum. Scale bar = 25 µm. Reprinted with permission from Turner and Boyle (1975); scanning electron micrograph courtesy of Ruth D. Turner.

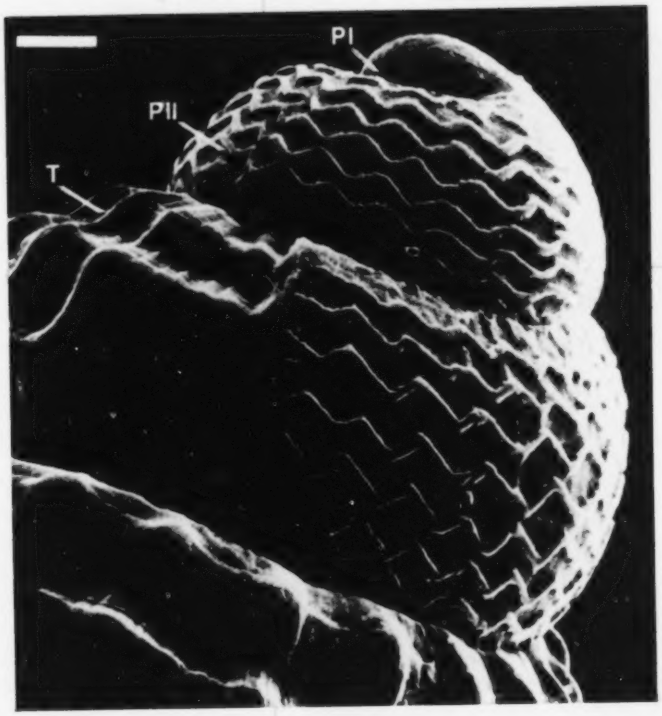

Figure 3. Scanning electron micrograph of Alvania jeffreysi (Rissoidae) showing gastropod larval shell terminology. PI, Protoconch I; PII, Protoconch II; T, teleoconch (post-larval shell). Scale bar = 50 µm. After Rodriguez Babio and Thiriot-Quiévreux (1974); micrograph courtesy of Catherine Thiriot-Quiévreux.

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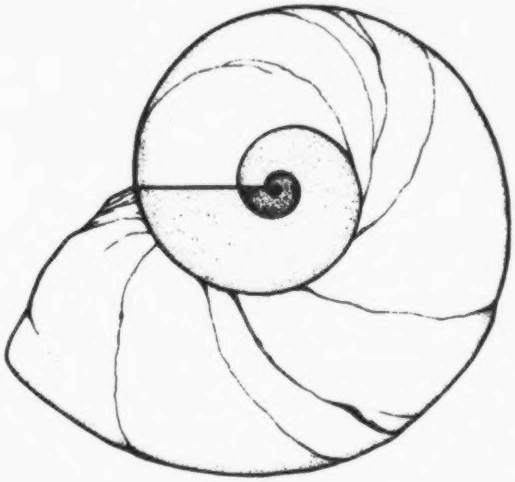

Figure 4. Method for determining number of protoconch whorls, following Taylor (1975). The sutural point at the aperture is counted as one whorl, with an additional whorl counted each time the reference line is crossed.

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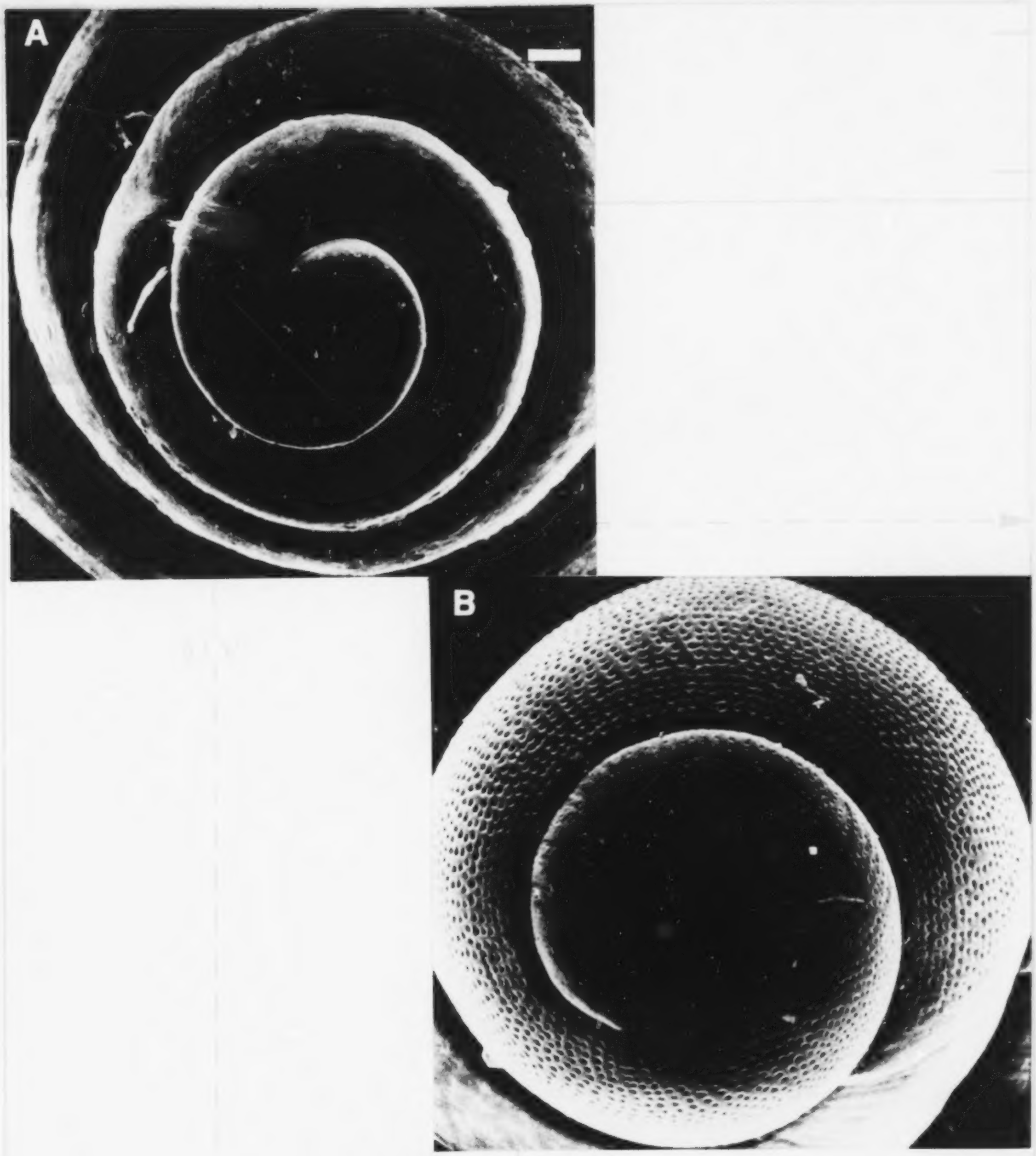

Figure 5. Protoconch morphology in rissoid gastropods of known developmental type. (A) Rissoa guerini, planktotrophic; (B) Barleeia rubra, nonplanktotrophic. Scanning electron micrographs at the same magnification; scale bar = 50 µm. Reprinted with permission from Thiriot-Quiévreux and Rodriguez Babio (1975); micrographs courtesy of Catherine Thiriot-Quiévreux.

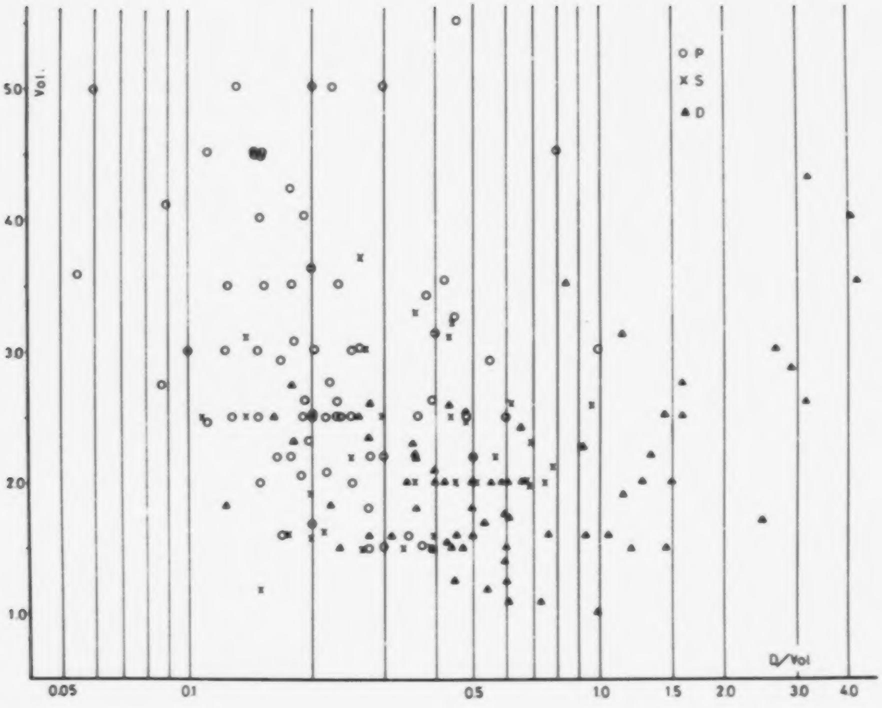

Figure 6. Relationship between developmental type and protoconch dimensions in prosobranch gastropods. Vol. = Number of volutions; D/Vol. = ratio maximum diameter to number of volutions. P = Planktotrophic larval type having moderate to long pelagic stage; S = planktotrophic larval type having short pelagic or demersal stage; D = directly developing lecithotrophic larval type. After Shuto (1974).

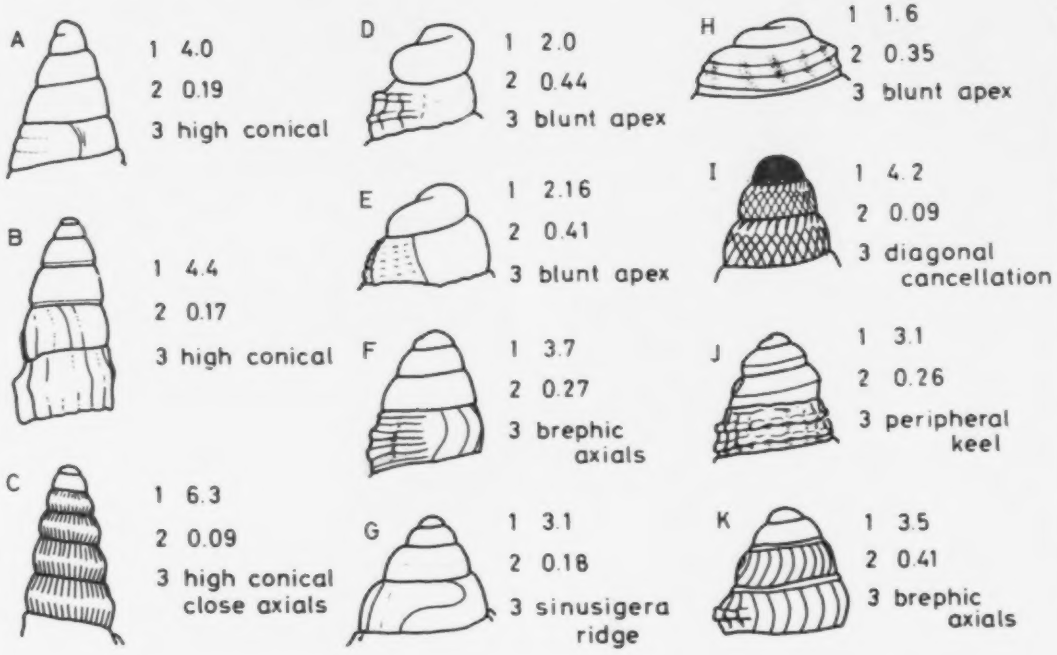

Figure 7. Relationship between morphology of protoconchs and of living and fossil prosobranch gastropods and developmental type. 1, Number of volutions; 2, Ratio of maximum diameter to number of volutions; 3, remarks. (A) Tiara gerthi philippinensis, Upper Miocene, inferred planktotrophic; (B) Triplostephanus santosi, Upper Miocene, inferred planktotrophic; (C) Triphora (Notosinister) conaspersa, Pleistocene, inferred planktotrophic; (D) Ocinebrellus eurypteron, Pleistocene, inferred lecithotrophic; (E) Merica asperella varicosa, Upper Miocene, inferred lecithotrophic; (F) Latirus (Dolicholatirus) fusiformis, Pliocene, inferred lecithotrophic; (G) Zafra pumila, Pleistocene, inferred planktotrophic; (H) Iwakawatrochus urbanus, Pleistocene, inferred lecithotrophic; (I) Philbertina linearis, Recent, planktotrophic; (J) Nassarius (Nassarius) caelatus verbeeki, Pliocene, inferred planktotrophic; (K) Gemmula (Gemmula) speciosa, Pliocene, inferred planktotrophic. Reprinted with permission from Shuto (1974).

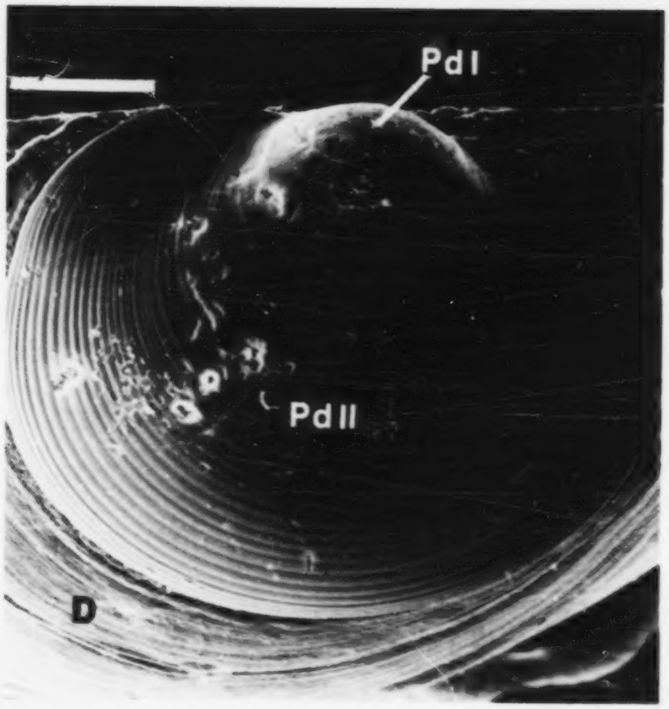

Figure 8. Bivalve larval and early juvenile shell terminology. PdI, Prodissoconch I; PdII, Prodissoconch II; D, dissoconch. Scanning electron micrograph is of the umbonal region of a deep-sea planktotrophic mytilid from a hydrothermal vent on the Galapoagos Rift. Scale bar = 100 µm.

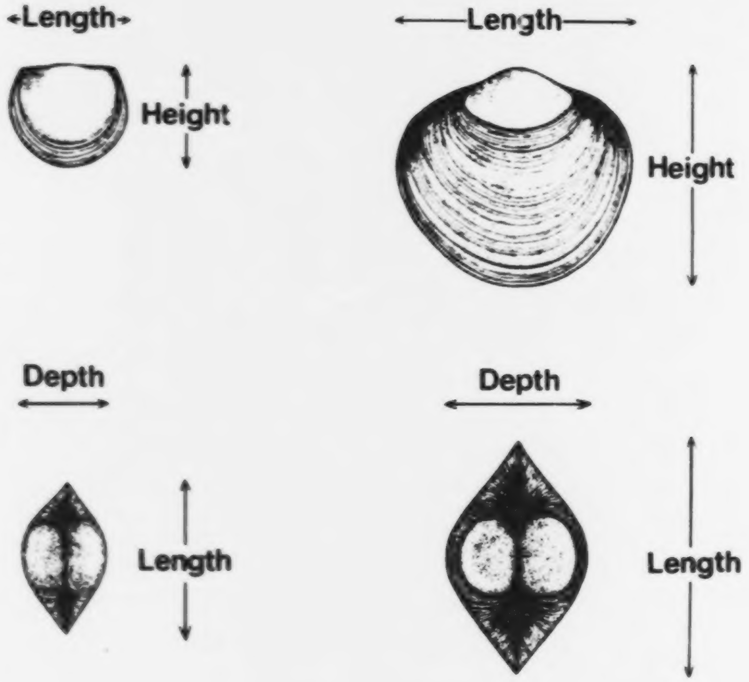

Figure 9. Bivalve larval shell dimension terminology. After Chanley and Andrews (1971).

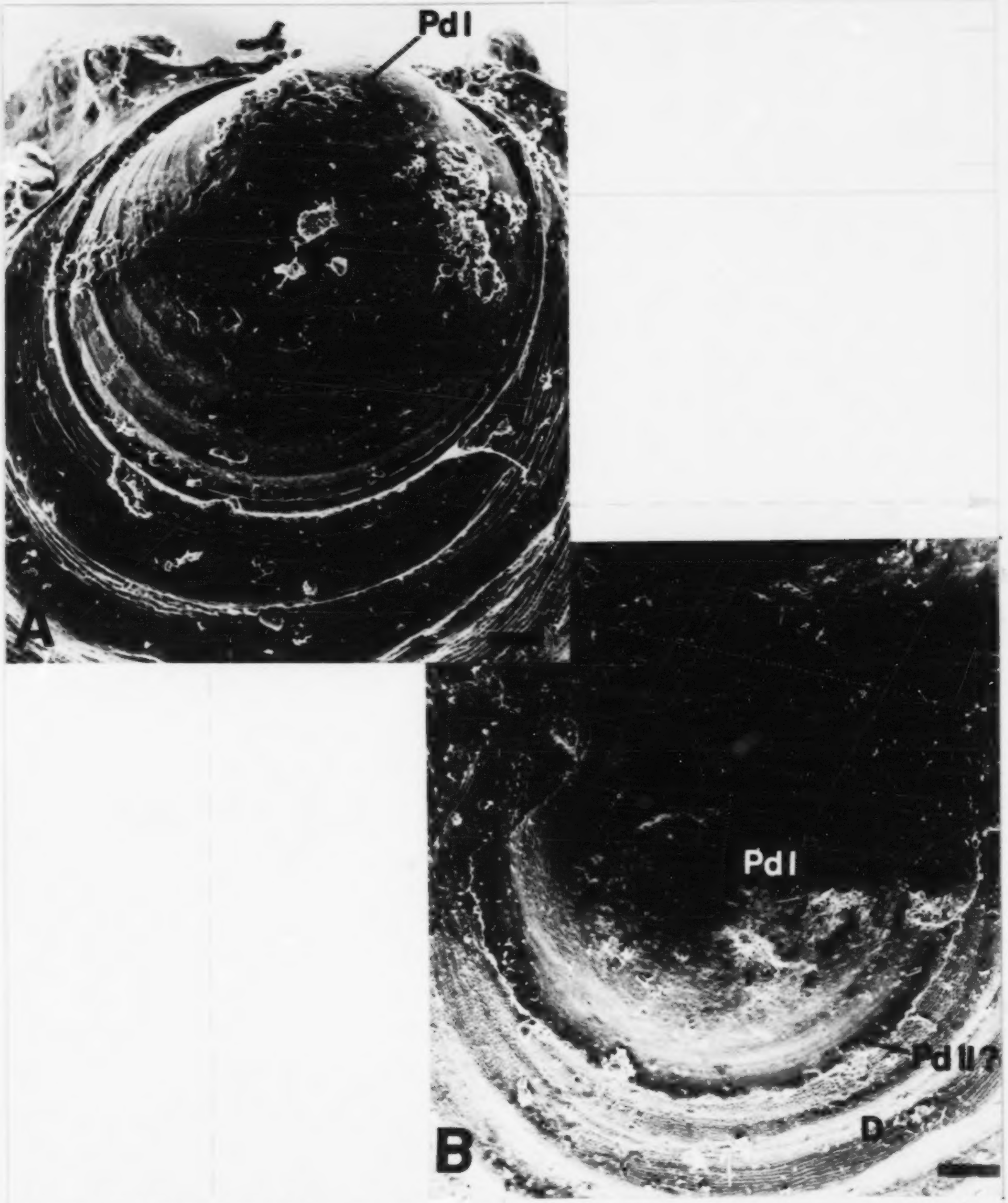

Figure 10. Scanning electron micrographs illustrating differences in larval shell morphology of two Late Cretaceous bivalves with different types of larval development. (A) Uddenia texana (planktotrophic); (B) Vetericardiella crenalirata (nonplanktotrophic). Scale bar = 20 μm.

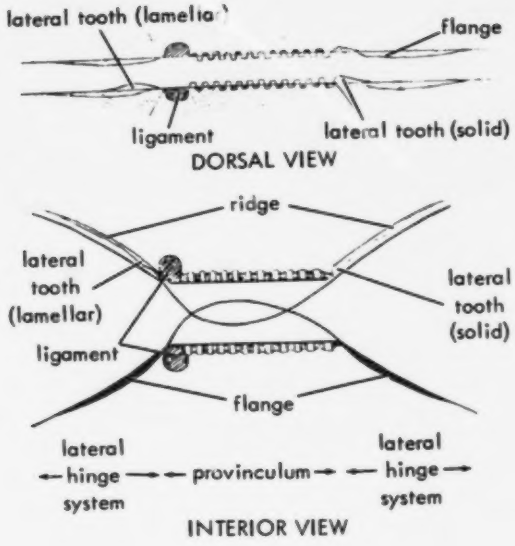

Figure 11. Terminology of bivalve larval hinge and associated structures. After Rees (1950); reprinted with permission from Cox (1969), courtesy of the Geological Society of America and University of Kansas Press.

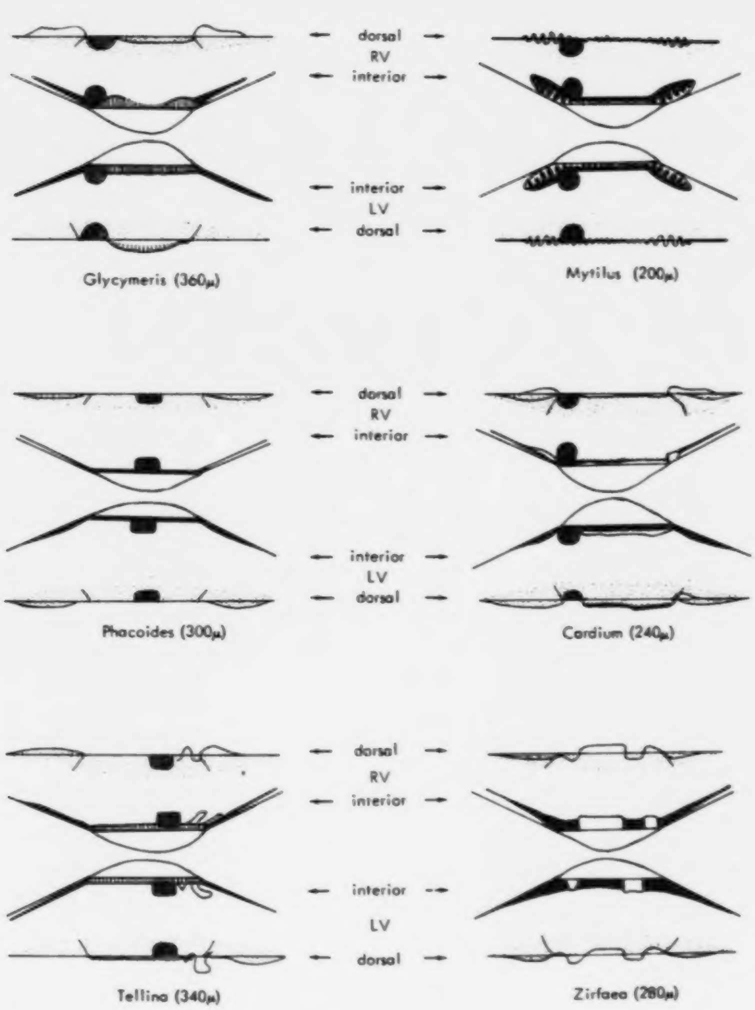

Figure 12. Prodissoconch hinges of six North Sea bivalve genera. After Rees (1950); reprinted with permission from Cox (1969), courtesy of the Geological Society of America and University of Kansas Press.

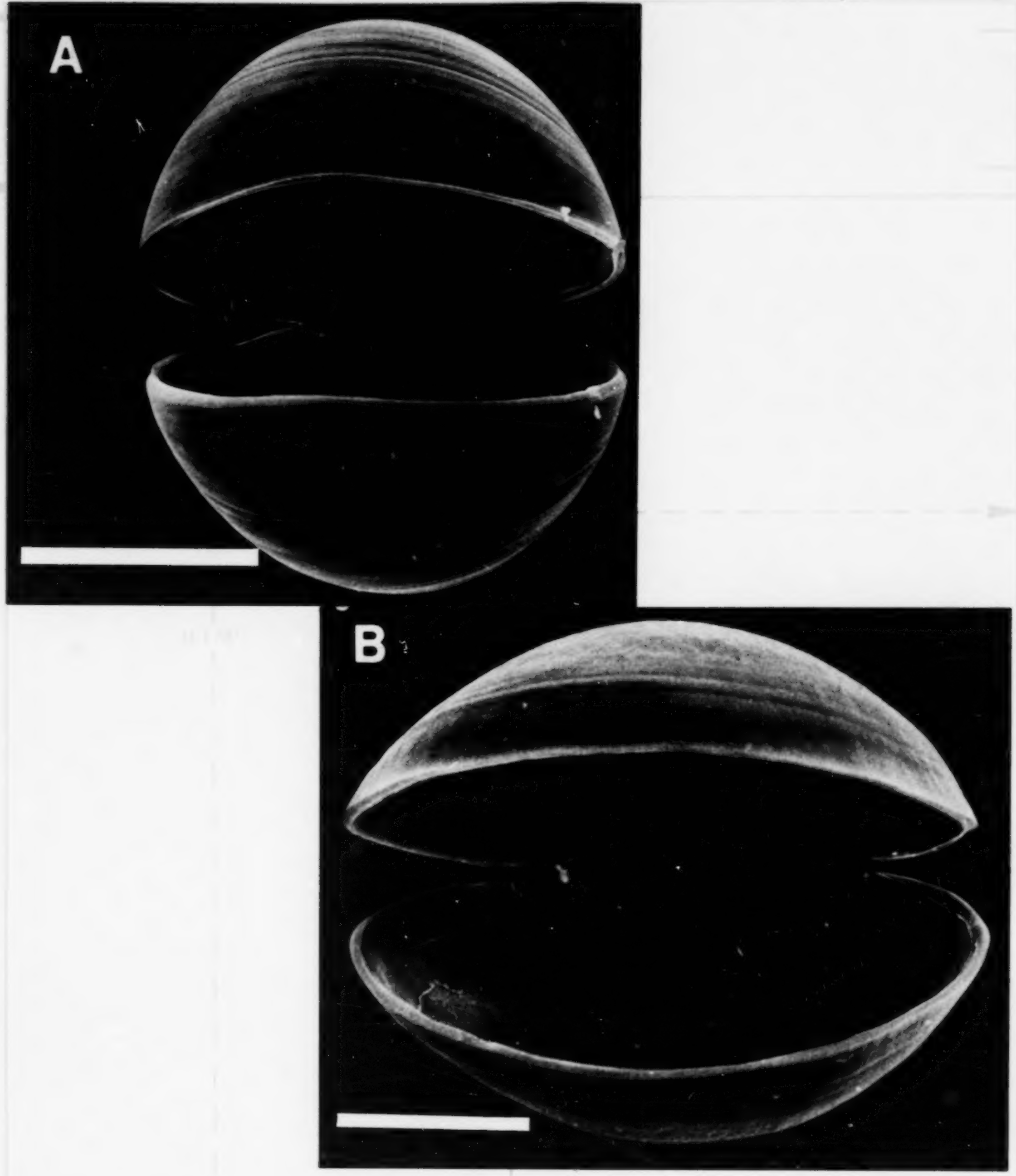

Figure 13. Scanning electron micrographs of bivalve larval hinge structures. Note distinctive hinge morphologies, diagnostic at superfamilial and lower taxonomic levels. (A) Teredo navalis (Pholadacea). Scale bar = 100 µm. (B) Ostrea edulis (Ostreacea). PdI, Prodissoconch I; PdII, Prodissoconch II; D, dissoconch. From Calloway and Turner (1979). Micrographs courtesy of C. Bradford Calloway and Ruth D. Turner.

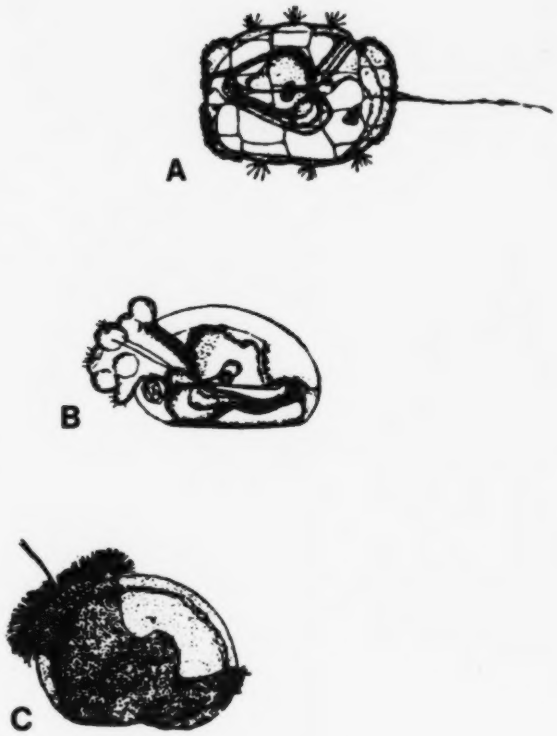

Figure 14. Unusual types of bivalve larvae. (A) Protobranch larva with ciliated test; Yoldia limatula Say. (B) Protobranch larva in the process of casting test; Yoldia limatula Say. (C) Pandoracean larva of Lyonsia hyalina (Conrad), showing indented hinge line. Drawings not to scale. From Chanley (1968).

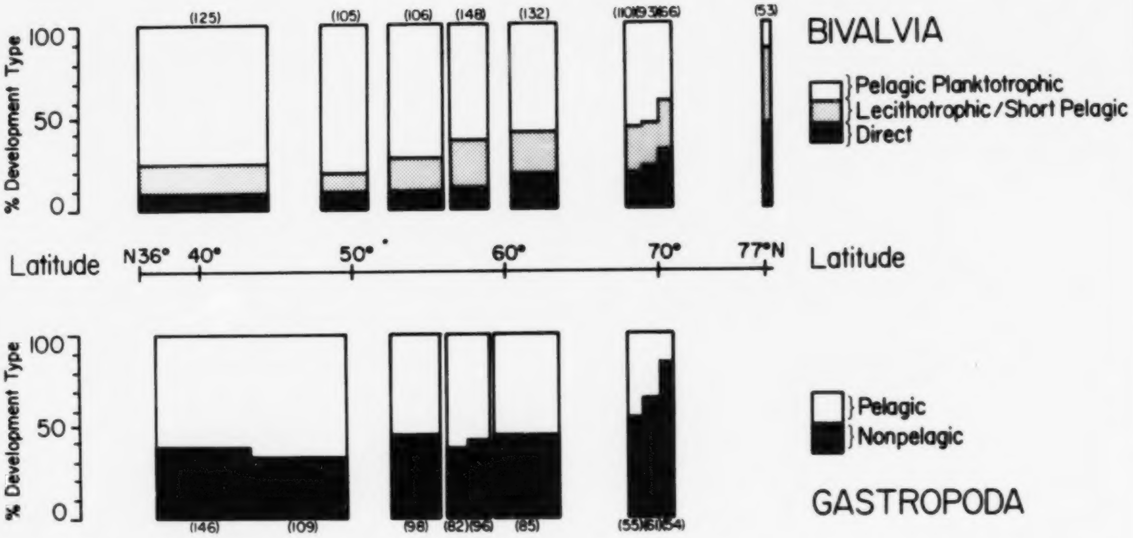

Figure 15. Molluscan developmental types as a function of latitude in the eastern North Atlantic. Bar widths delimit approximate latitudinal coverage of samples. Figures in parentheses indicate number of species. Subdivisions within bars indicate samples with overlapping latitudinal ranges. Bivalve data modified from Ockelmann (1965). Gastropod data modified from Thorson (1965).

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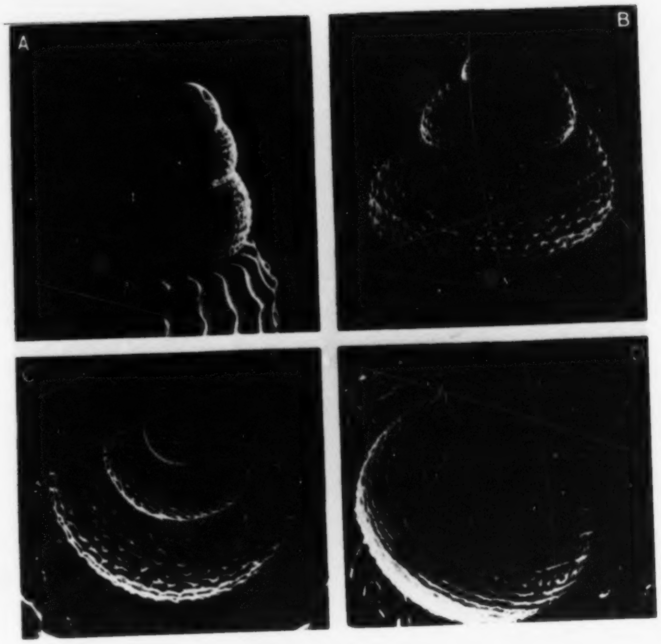

Figure 16. Apparent planktotrophy in deep-water gastropods. Scanning electron micrographs of Alvania cimicoides (Rissoidae) from a depth of 1050 m. Reprinted with permission from Bouchet (1976).

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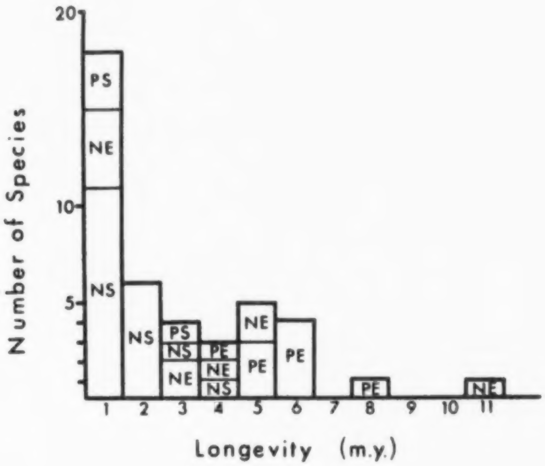

Figure 17. Developmental type and environmental tolerance of Lower Tertiary volutid gastropods and their relationship to species duration. N, nonplanktonic; P, planktonic; S, stenotopic; E, eurytopic; m.y., million years. Reprinted with permission from Hansen (1978). Copyright θ by the American Association for the Advancement of Science.

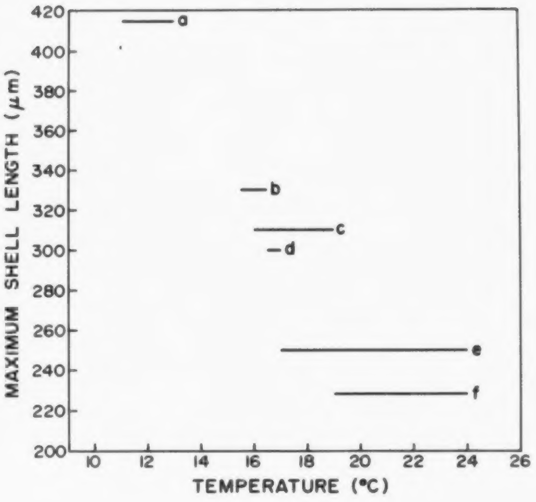

Figure 18. Relationship between environmental temperature and maximum shell length of larval Mya arenaria. a, St. Andrews, Canada; b, Hampton Beach, New Hampshire; c, laboratory culture by Savage and Goldberg (1976); d, Øresund, Denmark; e, Malpeque Bay, Canada; f, laboratory culture by Loosanoff and Davis (1963). Reprinted with permission from Lutz and Jablonski (1978). Copyright © by the American Association for the Advancement of Science.

Table 1
Rees' (1950) larval hinge type. Further subdivision of groups is possible using lateral hinge system, larval shell shape, etc.

	No Teeth	Few Teeth	Many Teeth
Provinculum Thick	________	Astartacea, some Cardiacea, some Solenacea, Hiatellacea, Myidae and some Corbulidae, Pholadacea	Mytilacea, Pectinacea, Anomiacea, Pteriacea, Ostreacea, Tellinacea, some Veneracea, some Mactracea
Provinculum Thin	Lucinacea Ercinacea	Some Cardiacea, some Mactracea, Pandoracea, Poromyacea	Some Cardiacea, some Solenacea, some Corbulidae

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CHAPTER 5

DEMOGRAPHIC ANALYSIS OF BIVALVE POPULATIONS

by

Robert M. Cerrato

Department of Geology and Geophysics
Yale University
New Haven, Connecticut
06520

CHAPTER 5

I. INTRODUCTION

A species possesses characteristics which cannot be expressed at the individual level, and which exist only in a statistical sense (Allee et al. 1949; Odum 1971). Such properties are termed group or population attributes (Allee et al. 1949). These quantities can be divided into two categories: (1) demographic characteristics associated with population structure and its maintenance (e.g. abundance, age structure, birth rates, age specific growth rates, mortality, etc.), and (2) genetic properties (i.e. adaptiveness, reproductive fitness, and persistence) (Odum 1971). Population attributes reflect the ecology of a species, and they can, therefore, provide information relevant to the study of the spatial and temporal extent of environmental stress. Accurate determination of one or more group attributes in natural populations is not a simple task. However, the potential for extracting these characteristics is particularly high if the organisms studied possess a calcareous skeleton.

In this chapter, I will use molluscan populations to illustrate how population attributes can be deduced from an analysis of shell parameters. The statistical unit of study will be the class-frequency histogram. As we shall see, many group attributes can be derived either directly or indirectly from an evaluation of this fundamental structure. This chapter will review, at an elementary level, methods of constructing and interpreting class-frequency histograms, present examples of specific techniques, and indicate how the derived information can be used for the analysis of environmental stress. Bivalve populations are given preferential treatment as their demographic properties have been extensively studied and this class is distributed throughout the marine ecosystem. In addition, I consider only shallow water populations living in a temperate or boreal climate.

II. CONSTRUCTION OF CLASS-FREQUENCY HISTOGRAMS

The simplest population characteristic to determine is species abundance. In many situations, a temporal or spatial analysis of abundance patterns yields useful information about an organism and its ecology. However, individuals within a population are not developmentally, physiologically or genetically identical, and may respond in different ways to various environmental stimuli. It is meaningful, therefore, to analyze a population at a higher level of resolution.

Population samples are most conveniently arranged for study by dividing the lifespan of the collected organisms into a number of non-overlapping groups, called classes. The class-frequencies for the sample are found by determining the number of individuals belonging to each class. A frequency table is usually constructed giving the class arrangement, i.e. the way in which the classes were defined, and the corresponding class frequencies (Table 1). The graphical equivalent to the frequency table is the frequency histogram (Figure 1). Terms commonly used to describe the qualitative shape of class-frequency histograms are shown in Figure 2.

For molluscan populations in which shell microstructural growth patterns are clearly defined (see Chapters 2 and 3), the class arrangement may be based on age. Age-class intervals may be chosen to distinguish year classes, recruitment events, or they may represent even smaller periods of time. When reliable age estimates are not available, class-frequency histograms may be based on other shell parameters such as antero-posterior length, shell width, or height. Size-class intervals are normally quite small and generally range from 1 to 5 per cent of the size of the largest individual in the population. Size-frequency histograms are useful even when ages can be determined. By constructing histograms with small size-class intervals, variations in growth within a year or recruitment class can be resolved. Size-frequency histograms may, therefore, provide additional details about age-specific growth dynamics.

III. INTERPRETATION OF CLASS-FREQUENCY HISTOGRAMS

In the following paragraphs, I will show how population attributes may be derived from class-frequency histograms. Many of these attributes are time-specific (e.g. seasonal recruitment, age-specific growth and mortality). It is important, therefore, to relate class assignments to real time. As we shall see, many of the analytical techniques discussed are devoted to establishing this relationship.

Recruitment, Growth, and Age Structure

For populations of molluscs living in a temperate or boreal climate, recruitment is often seasonal with one or more distinct spawning periods during the year. However, unless one can frequently sample a population during the spawning season(s), estimates of recruitment commonly depend on a knowledge of other population attributes. For example, consider a hypothetical sedentary population in which the spawning season is restricted to a four week period beginning in June. Let us also assume that recruitment and mortality do not vary from year to year. For such a population, a representative age-frequency histogram obtained from a census collected in July, that is, just after the cessation of spawning, is given in Figure 3a. The decreasing pattern of abundance with age in this example is due only to mortality. If this same population were sampled six months later, say in January, it might appear as shown in Figure 3b. No recruitment has taken place during the intervening period and the size of each cohort is further reduced by mortality.

Variations in both recruitment and mortality will complicate this simple picture. A quantitative assessment of spatial and temporal recruitment patterns is possible only if losses due to mortality can be accurately estimated. In addition, older age-classes usually comprise only a small percentage of the total sample, and they are especially prone to collection bias. Thus only the more recent recruitment events can ordinarily be used in an analysis.

Exceptional departures from normal recruitment patterns are the easiest to recognize. Such an event can often be identified for a considerable period of time after it occurs. For example, the poor numerical representation of the 2+ year class of *Spisula solida* (Figure 4) suggests weak recruitment two years prior to the census date. As a second example, consider the age structure of the bivalve *Venerepis pullastra* in Figure 5. If an unusually large and successful spawning event(s) takes place, recruitment in subsequent years may be suppressed (Odum 1971). Thus it is possible for a population to be numerically dominated by one or a few large, older age-classes. The age structure of *Venerepis pullastra* (Figure 5) may reflect this dominant age-class phenomenon.

When age determinations are not available, shell size parameters form the basis for class-frequency histograms. Size-frequency histograms are common in the literature on molluscan populations. They are easy to construct, and require less subjective judgment than counting and interpreting shell growth increments.

The shape of a size-frequency histogram is influenced not only by recruitment and mortality, as I have illustrated with age-frequency distributions, but by ontogenetic growth rates as well. The relationship between a size parameter such as antero-posterior length and the age of a mollusc is non-linear and species specific. The growth curve is often sigmoidal in form (Figure 6), but there is no general model that can account satisfactorily for all the different types of growth curves that are observed. The size-age relationship also depends on many environmental factors. Temporal and spatial variations in average rates of shell growth are often evident. For example, average growth curves, reported by Seed (1976) for several populations of *Mytilus edulis*, are shown in Figure 7. For a complete review of those environmental factors which may influence shell growth rates, the reader is referred to Hallam (1965).

Within a population, individuals of the same age will not be the same size. When a cohort is plotted as a size-frequency histogram, it will generally appear as a normal or slightly positively skewed distribution (Craig and Hallam 1963). The degree of variation in size between individuals in the same age class (cohort) will usually increase in proportion to the mean or average length (Simpson and Roe 1939; Craig and Hallam 1963).

Because recruitment is seasonal, a size-frequency histogram will be polymodal with each peak representing one or more spawning events. The general form of size-frequency histograms is illustrated in Figure 8. In this hypothetical example, the individual recruitment classes making up the histogram are included for clarity. The trend of increased dispersion in older recruitment classes is qualitatively characteristic of most distributions. The size-frequency histograms shown in Figure 8 have the same age structure as the hypothetical population in Figure 3. Figure 8a shows the population as it would appear in July, just after annual recruitment. The most recent cohort has been labeled the 0+ year class. Figure 8b shows the same population as it might appear in January. The size modes are all displaced to the right as a result of six months' growth. Once the position of each peak is determined, the relationship between size and absolute time can be established. One can construct an estimate of the average ontogenetic growth curve from this information (Figure 9).

For molluscan populations much information about recruitment, growth, and age structure can be obtained from size-frequency histograms. For example, Figure 10 is a temporal sequence of size-frequency histograms for the bivalve *Donax incarnatus*. Two year classes are present in the samples. These are easily identified and followed in time. By plotting mean shell length for both year classes vs. time, an average growth curve for this population is derived (Figure 11).

As a second example, I have chosen a population of *Mytilus edulis* (Figure 12). Age class assignments given in this figure were determined by Craig and Hallam (1963) on the basis of mode identification, supplemented by growth data collected in this same general locality by Savage (1956). Recruitment classes are not as clearly defined as in the previous example. Based on Savage's growth data (Figure 13), the peak of the 1+ year class in the April 1961 sample should have been located at about 12 mm. Absence of a mode here suggests inadequate sampling and poor annual recruitment during 1960 (Craig and Hallam 1963). The 1960 cohort appears to be represented as a small minor mode in the November 1961 sample (Craig and Hallam 1963), but no clear interpretation can be made.

In this example, only the more recent spawning events are sharply defined. Because of size dispersion within a recruitment class, and because of the marked decrease in growth-rate with age in *M. edulis*, older age groups tend to merge together. Because of the decreasing ontogenetic rates of growth with age, Craig and Hallam (1963) suggest that typical size-frequency histograms will have up to three clearly separated peaks at any season. This is an ideal upper limit as they also point out that the number of clearly defined modes may be reduced by poor recruitment in some years, by mortality, or if sampling takes place a long period of time after the most recent spawning event. The recognition of peaks in size-frequency histograms represents, therefore, a very important aspect in determining information about recruitment, growth, and age structure in populations.

Recognition of Age Classes in Size-Frequency Distributions

A useful technique for distinguishing between separate age-classes in a size-frequency histogram is due to Sheldon (1965). This method is based on earlier work by Walford (1946). For many shellfish species, Walford determined that a plot of the size of an individual at any given age (L_t) against its size one year later (L_{t+1}) is approximately linear (Figure 14). In addition, he found that the line produced intercepts a point of no growth, that is, a point at which $L_t = L_{t+1}$).

Consider a size-frequency histogram in which only the modes of the first two recruitment classes are clearly defined. Sheldon's method for recognizing other modes in the distribution is the following: the average sizes of the two initial modes are plotted as a point on a graph of L_t vs. L_{t+1}. Using an estimate of the mean size of the oldest age class in the population, a second point located at $L_t = L_{t+1}$ is also plotted. For this point, Sheldon proposes taking that size class which is larger than 98 per cent of the individuals in the population. By drawing a line between these two points, the position of successive modes can be estimated. Starting on the abscissa with the average size of the last discernible mode, the approximate location of the next year class may be read off the line. This process is generally repeated several times using the current estimate to predict the average size of the next older age class.

A fossil example of this method applied to the brachiopod *Chonotes laguessiana* is shown in Figure 15. The average size of the first two modes were estimated by Sheldon (1965) to be 0.25 and 0.69 cm respectively. These modes are assumed to represent two separate year classes. The mean maximum size was taken by Sheldon to be 1.22 cm. Figure 16 shows a straight line joining the two points: (1) L_2 plotted against L_1, and (2) the mean maximum size, i.e. $L_t = L_{t+1}$. From this line, one can determine that the peak of the third year class should be located at 0.93 cm. By referring to Figure 15 we see that a mode is located at approximately the same position as predicted. Peaks corresponding to a fourth or fifth year class cannot be recognized in the size-frequency histogram. Their presence may have been obscured by the merging effect common in older age groups. In many cases it will be important to distinguish the numerical contribution of individual recruitment classes when they overlap as they do in this example. The problem of overlapping age classes in size-frequency histograms is discussed in the next section.

To demonstrate the usefulness of the technique in evaluating recruitment, consider the size-frequency histogram of the bivalve *Spistula solida* in Figure 17. The location of the first two modes, and an estimate of the mean maximum size, can be used to form a Walford plot (Figure 18). This plot predicts a mode for the 1970 year class at about 38 mm. Absence of a mode supports the conclusion by Smith (1975), based on growth ring analysis, that recruitment was poor in 1970.

Quantitative Estimate of Age-Classes From Size-Frequency Distribution

Because the shape of most age-classes approximates a normal distribution, one can make effective use of probability paper in distinguishing separate modes in a polymodal size-frequency histogram. This technique is, unfortunately, seldom used in population studies. I will, therefore, consider this method in detail.

First we will consider how a normal or gaussian distribution plots on standard probability paper. A size-frequency distribution made up of 1572 measurements is shown in Figure 19. Data from this histogram are plotted on probability paper as cumulative percentages. For example, the first size class consists of one individual. Therefore, $\frac{1}{1572}$ x 100 or .06% of the sample falls below 19.25 mm in length. This point is plotted as P_1. The second class consists of three individuals, and so $\frac{3+1}{1572}$ x 100 or .25% of the population lies below 1975 mm in length (P_2). The second class consists of three individuals, and so $\frac{3+1}{1572}$ x 100 or .25% of the population lies below 19.75 mm in length (P_2). The third class has 30 individuals, so $\frac{30+3+1}{1572}$ x 100 or 2.2% lies below 20.25 mm (P_3). The fourth class has 39 individuals, hence $\frac{39+30+3+1}{1572}$ x 100 or 4.7% lies below 20.75 mm (P_4). This process is continued for all the classes in the distribution. Thus class length vs. cumulative frequency plots as a straight line for a normal distribution.

Population parameters may be derived from this line. The mean of the sample is estimated as the size at the 50% probability point (M). The standard deviation is found by subtracting the size at the 84.13% probability point (S_2) from the 15.87% probability point (S_1) and dividing by 2. In this example,

$$\bar{x} \equiv \text{mean} = L_{50\%} \doteq 22.35 \text{ mm},$$

$$s = \text{standard deviation} \equiv \frac{L_{84.13\%} - L_{15.87\%}}{2}$$

$$\doteq (23.4 - 21.35)/2$$

$$= 1.05 \text{ mm}$$

The percentages ($L_{50\%}$, $L_{84.13\%}$) are the same for any normal distribution.

A class-frequency distribution that is multimodal, but made up of a number of overlapping normal distributions, will not plot as a straight line on probability paper. The characteristic shape of a bimodal normal distribution is sigmoidal (Figures 20 and 21) with the curve having a single point of inflection (located at 50% in Figure 20, and at 97% in Figure 21). In general, the number of points of inflection will be one less than the number of modes making up the distribution. In Figure 22, there are four points of inflection located at 10, 66, 91, and 98.6% respectively. We therefore expect the population in this figure to be composed of five overlapping normal distributions.

The process of separating modes from one another will be illustrated using Figure 22. The first mode in the original distribution is extracted by multiplying the original percentages of all the points up to the first point of inflection by 100 divided by the percentage of the first inflection point. In this case, the location of the first inflection point is 10%, and so one multiplies by 100/10. Thus for the first point (P_1), the original percentage is 2.3%, therefore,

$$P_1 = 2.3\% \times \frac{100}{10} = 23\%.$$

For the second point (P_2), the original percentage is 5.1%, therefore,

$$P_2' = 5.1\% \times \frac{100}{10} = 51\%$$

For the third point (P_3), the original percentage is 8.6%, therefore,

$$P_3' = 8.6\% \times \frac{100}{10} = 86\%$$

Finally, for the last point (P_4), the original percentage is 9.8%, therefore,

$$P_4' = 9.8\% \times \frac{100}{10} = 98\%.$$

These newly calculated percentages are then plotted with their appropriate lengths, and the resulting line, denoted by A in Figure 22, is the distribution of the first mode. It has a mean of about 3.22 mm and a standard deviation of 0.27 mm. It makes up a total of about 10% of the original population as determined from the location of the inflection point.

The second mode is extracted in a similar way except that the location of the first inflection point must be subtracted both from the original percentages, and from the location of the second inflection. All points located between the first (10%) and second (66%) inflection points are used. For example, the first point (P_5) beyond the first inflection is located at 10.9%, therefore,

$$P_5' = \frac{\text{(original percentage - location of first inflection}}{\text{(location of second inflection - location of first inflection}} \times 100 =$$

$$\frac{(10.9 - 10.)}{(66. - 10.)} \times 100 = 1.6\%.$$

For the second point (P_6) beyond the first inflection:

$$P_6' = \frac{(12.5 - 10.)}{(66. - 10.)} \times 100 = 4.4\%.$$

When all these points are plotted, they yield the straight line labeled B in Figure 22. The second mode has a mean of 5.33 mm and a standard deviation of 0.62 mm. It comprises (66 - 10) or 56% of the original population.

The third mode is extracted using points located between the second and third inflection points, and percentages determined from:

$$P_i' = \frac{\text{(original percentage - location of second inflection)}}{\text{(location of third inflection - location of second inflection)}} \times 100.$$

The resulting line is labeled C in Figure 22.

The fourth mode is determined in a similar way (line D). The fifth mode is too small to resolve.

For small samples, i.e. less than 25 measurements, it may not be possible to define meaningful class assignments. However, the data set may still be plotted on normal probability paper. With small samples, individuals are arranged according to increasing size. The cumulative percentage of the i'th point in this ordered sample is then simply i/n x 100, where n is the number of individuals in the sample. Plotting these cumulative percentages vs. size will generate an acceptable probability plot. Note, however, that when a sample is plotted in this way, the last point will have a cumulative value of 100 per cent. This point cannot, therefore, be included in the analysis. To correct for this problem, Guttman and Wilks (1965) suggest that 100/2n be subtracted from the cumulative percentage of all points.

Size-frequency histograms are sometimes truncated at one or both ends. Truncation may occur, for example, when benthic samples are sieved, and the mesh size used is larger than the smallest individuals in the population. A truncated mode will not plot as a straight line on probability paper. To correct for truncation in a given mode, the following equations may be applied (Cassie 1954). For truncation on the small size end,

$$p' = p(1 - p''/100) + p'',$$

where p is the uncorrected cumulative percentage, p' is the corrected cumulative percentage, and p" is an estimate of the percent truncation. For truncation on the large size end,

$$p' = p(1 - p''/100).$$

Mortality

Information on mortality is generally summarized in a life table. A life table is simply a columnar tabulation of statistical quantities relating to survivorship, rates of mortality, and the mean expectation of life (Table 2). The information appearing in a life table is stated as a function of the age of the organism, where age itself may be expressed in absolute terms (in months, years, etc.), or in relative terms by comparing one part of the life cycle with another (Kurtén 1964; Levinton and Bambach 1969). The statistical quantities appearing in a life table are formally defined as:

x = age;
x' = age as a percent deviation from the mean length of life;
l_x = the number of survivors at the start of age interval x;
d_x = the number dying during the age interval x to x + 1;
q_x = the rate of mortality during the age interval x to x + 1;
L_x = the average number of individuals alive during the age interval x to x + 1;
T_x = the number of individual time units left in the population at the start of age interval x;
e_x = the mean expectation of life for an organism at the start of age interval x.

The standard practice is to normalize the population at age zero to 1000 individuals (Table 2). Not all of the columns shown in this example appear in a given life table. T_x and L_x are often omitted.

The above statistical quantities are computed from observations of either l_x or d_x (Table 3). Information about mortality may be obtained from three sources. These sources reflect different sampling strategies, and they may be classified as (Deevey 1947):

(1) Direct observations of the age at death (d_x). This strategy generally requires a census of the death assemblage.

(2) Direct observation of survival (l_x) in the life assemblage. Individuals of a specific age class (cohort) are identified and followed in time by periodic sampling.

(3) Indirect observation of the age at death (d_x). A census of the life assemblage is collected at a given time. The quantity d_x is inferred from the numerical differences between successively older age classes.

Certain problems associated with mortality data are important to mention at this point. Factors affecting the death assemblage such as transport or differential shell destruction will tend to bias the results in case (1). Furthermore, to use cases (1) and (3) safely one must assume that the living population is stable in time (Deevey 1947). To insure this, it may be necessary to average a time sequence of class-frequency histograms (Levinton and Bambach 1969; Deevey 1947). Finally, the application of case (2) will avoid most of the above problems, but it will give mortality information for only one age class. While this may be desirable in many specific situations (such as following the mortality effects of a pollution event), the resulting life table may or may not represent the mortality patterns of the entire population. However, averaging the life tables of several cohorts is usually acceptable in this situation.

Because one cannot screen out all of the above problems, life tables constructed for the same population, but using different sampling strategies will yield somewhat different results.

Survivorship

In an analysis of mortality, it has become traditional to concentrate on one particular statistical quantity, l_x, the survivorship. Survivorship is conveniently displayed by plotting l_x on a logarithmic scale as a function of age (x), or age as a percent deviation from the mean length of life (x').

Various types of theoretical survivorship curves are shown in Figure 23. They have been discussed in general by many authors, including Pearl (1940), Deevey (1947), Craig and Hallam (1963), Kurtén (1964), and Craig and Oertel (1966). Curve I is the negatively-skewed rectangular type, and represents a population with low mortality early in life, but with high mortality in old age. Curve II is diagonal and characteristic of constant mortality throughout life, i.e. age independent mortality. Curve III, the positively-skewed rectangle, is found in populations with high mortality in the youngest growth stages. Curves Ia and IIIa are less extreme versions of I and III.

Kurtén (1964) suggests that the survivorship patterns shown in Figure 23 are approximated in nature only during a portion of the entire life span of an organism. When the complete record of a species population is considered, including all larval, juvenile, and adult stages, the shape of the survivorship curve is sigmoidal (Figure 24), with high mortality in both young and old age classes (Kurtén 1964).

I have chosen several examples from the literature to illustrate survivorship. The first example is the California Pismo Clam, *Tivela stultorum*, studied by Fitch (1950). Censuses of living populations collected over several years allowed Fitch to estimate mortality. From this information, Hallam (1967) constructed a life table (Table 2). The survivorship curve (Figure 25) taken from this life table has a sigmoidal form even though mortality was estimated only after spat settling. As noted by Hallam, mortality is high during the first year, begins to decline, and then sharply increases again after the fourth year of life. Man has had a major effect on the shape of this survivorship curve. At about four years of age, the clams reach a marketable size (Hallam 1967). Without human predation, an individual may live for 35 years or more (Hallam 1967).

In another example, Craig and Hallam (1963) studied mortality in the mussel *Mytilus edulis* from the coast of Great Britain. Mortality data was obtained from size-frequency histograms of dead shell assemblages (Figure 26). Age was estimated from growth data provided by Savage (1956) (Figure 13). Only post-larval individuals were considered in the mortality data, hence, the survivorship curves from the two localities are not sigmoidal (Figure 26). The curves indicate that the mortality factors of Ferny Ness and Craigelaw Bay act on the live populations in similar ways.

The final example to be considered is from Levinton and Bambach (1969). When constructing life tables or survivorship curves, the age of individuals in a population must be known. An erroneous estimate of age will make the tabulation of mortality inaccurate. When other methods of absolute aging fail, Levinton and Bambach (1969) propose application of a technique developed specifically for bivalves that may be used to assign an approximate relative age scale to individuals in a population. Levinton and Bambach (1969) have observed that a relative growth model given by the logarithmic relation,

$$D = s \ln (T + 1)$$

where D is the size, T is the relative age, and s is a constant, seems to account adequately for a number of growth curves found in Hallam (1967) (Figure 27). Their technique is simple to apply. If a relative age at a particular size is chosen, s may be determined. The relative age of any other individual may then be estimated from the inverse to the above equation, i.e.

$$T = e^{D/s} - 1.$$

For example, suppose we wish to give the largest individual in a population a relative age of 10. If the size of this individual is 54.30 mm, then s becomes,

$$s = \frac{D}{\ln(T + 1)} = \frac{54.3\text{mm}}{\ln(10 + 1)} = \frac{54.30}{2.398} \doteq 22.64.$$

From the inverse equation, the relative age of an individual 40.00 mm long is then

$$T_{D = 40.} = e^{D/s} - 1 = e^{40/22.64} - 1 \doteq 4.85.$$

In Levinton and Bambach (1969), information on mortality for two bivalve species was derived from size-frequency histograms of the death assemblage. Relative age was determined by the above method. The smallest size classes in all sampled death assemblages were lost by sieving. The two species considered were: Yoldia limatula, an infaunal deposit feeding nuculanid, and Mulinia lateralis, an infaunal filter feeding mactrid. All populations were collected from shallow-water, muddy-bottoms in central Long Island Sound.

Two survivorship curves for Yoldia are shown in Figure 28. Higher juvenile mortality in the second Yoldia population was attributed to substratum stability. This sample was collected in an area which had a thin (1 cm.), noncohesive, mobile layer at the sediment-water interface (Levinton and Bambach 1969). This zone provided poor physical support for juveniles (Levinton and Bambach 1969). Adults, because they have the capacity to live in the more cohesive substratum below this zone, were not affected (Levinton and Bambach 1969).

A survivorship curve obtained for Mulinia by Levinton and Bambach (1969) is given in Figure 29. Mulinia appears to show higher juvenile mortality than Yoldia. Levinton and Bambach ascribe this to the observation that juvenile filter feeders are especially sensitive to high levels of suspended sediment.

The examples from Craig and Hallam (1963) and from Levinton and Bambach (1969) are interesting because they explicitly use the death assemblage to estimate mortality. The survivorship curves are, however, inaccurate in each case. The growth curves used to estimate age are one source of concern. There are no assurances that the size-age relationship is accurate for any specific population in these examples. In addition, variations in size between individuals of the same age were not considered in either paper.

In both papers, the raw size data is transformed so that no reinterpretation of the survivorship method is needed for the analysis. No attempt should be made to compare the resulting curves to ordinary survivorship curves. The methods used in these examples produce only an analog of "true" survivorship. I believe, however, that the analogy is a potentially useful one. The alternative would be to develop a reliable stochastic model of shell growth. This is not easily done.

For many species, and for molluscs in particular, mortality is dependent more on size than on absolute age (Emlen 1973). Thus it is entirely appropriate for comparative purposes to construct "size" survivorship curves directly from the raw data. The nonlinear transformations used by Craig and Hallam

(1963) and by Levinton and Bambach (1969) appear to be consistently applied, but they are not necessary. In either the transformed or in the untransformed cases, the conclusions reached can be safely interpreted only in terms of "size" survivorship. Either case does, however, provide useful information about mortality.

Further Uses of Death Assemblages

Death assemblages may be used to obtain other information on population attributes under one of two conditions. First, if mass mortality occurs, the dead shell assemblage created by the event represents a quantitative census of the living population (Levinton and Bambach 1969; Kurtén 1964). Population attributes prior to the event can be evaluated just as if the population were still alive. These estimates can be used later to assess the extent of population recovery by newly settled individuals. Care must be taken to exclude shells not associated with the single mortality event, because the mixture would destroy the features of the census. Growth increment patterns may be used to reject all shells that do not have the same season of death (see Chapters 2 and 3).

Secondly, if relatively high mortality occurs during a season of slow or little growth, then the death assemblage will tend to resemble the size-frequency distribution of the living population (Sheldon 1965; Craig and Oertel 1967). The season of slow growth for molluscan populations is during the winter. When mortality is high enough, and when there is little "contamination" of the sample by shells of individuals that did not die during this period, the death assemblage becomes a biased census of the population. The census is biased because mortality is age (or size) specific. If a correction for this bias is made, the data can be used just as if it were a winter census of the living population.

To justify this assertion, consider in Figure 30 the size-frequency histograms of live Cardium edule and articulated and disarticulated death assemblages of C. edule collected as a census by Craig and Hallam (1963). Cardium has clearly defined winter growth rings; a histogram of growth ring size-frequencies from the living population is also included in Figure 30. The living population at Peffer Burn is uni-modal and represents essentially one cohort. Two peaks (14.5 and 21.5 mm) in the growth ring size-frequency histograms coincide with peaks in the shell death assemblages.

Disarticulation may be attributed to the gradual decomposition and disintegration of the ligament joining the two valves together (Craig and Hallam 1963). In this example, individuals dying in the more recent winter (1961) are represented to a large extent by articulated shells. Those dying in the previous winter (1960) are mostly disarticulated. A two year record of the population during the winter is clearly preserved, therefore, in this death assemblage.

Adaptiveness

The genetic properties of a population (adaptiveness, reproductive fitness, and persistence) cannot be determined from a short term analysis of class-frequency histograms. However, because of an interesting correlation, one genetic property, adaptiveness, can be qualitatively inferred from population attributes already discussed. If one studies the biological attributes of species populations colonizing "new" or recently disturbed habitats, it is possible to recognize patterns in survival adaptations (Odum 1969; Rhoads, McCall, and Yingst 1978). These patterns of adaptation are remarkably similar in taxonomically distinct organisms, and can be observed in terrestrial as well as marine species (Hutchison 1953; Margalef 1958). One aspect of adaptation is the relationship between population attributes and habitat stability.

An organism colonizing a new or short-lived unpredictable environment is able to: (1) discover a suitable habitat quickly because of a high dispersal capacity; (2) grow, mature, and reproduce quickly before other organisms enter the habitat and compete for resources; and (3) either disperse quickly or suffer high mortality as resources decline or are used up (Wilson and Bossert 1971). Such a species is an opportunist. Opportunists are adapted for life in biologically unsaturated community (Pianka 1970). They have followed an evolutionary pathway which favors a high intrinsic rate of increase at the expense of competitive ability. An opportunist is often called an r-strategist, a reference derived from the logistic equation of population growth. In the logistic equation, the symbol r represents the intrinsic rate of increase of the population.

An organism adapted to a stable environment has less need for rapid dispersal, growth, or reproductive capabilities (Wilson and Bossert 1971). In stable habitats, population abundances are close to the carrying capacity of the environment (Pianka 1970). To maintain itself in such an environment, an organism is dependent primarily on its ability to compete for resources. Here, natural selection favors increased specialization at the expense of a high reproductive capacity. An organism adapted to a stable environment will, therefore, be a specialist. A specialist is often called an equilibrium species or a k-strategist, a term which again refers to the logistic equation of population growth. In the logistic equation, k is a symbol which represents the carrying capacity of the environment.

Correlates of r- and k- selection are found in Table 4. These strategies represented opposite ends of a continuous spectrum which runs from unstable or unpredictably changing environments dominated by opportunists to stable or relatively constant environments dominated by equilibrium species (e.g. Sanders and Hessler 1969; Slobodkin and Sanders 1969; Pianka 1966; Klopfer and MacArthur 1961). Most species will lie somewhere between these two extremes.

The r and k correlates in Table 4 may be used to place species in a relative order of opportunism. For example, consider two species commonly encountered in Long Island Sound: Mulinia lateralis and Nucula annulata. Mulinia lateralis is characterized by rapid development, a short generation time, and a life span rarely exceeding 3 years. Nucula annulata develops more slowly, has delayed reproduction, and has a life span sometimes exceeding 8 years in Long Island Sound. One would expect, therefore, that Mulinia is more opportunistic than Nucula. This is observed in Long Island Sound. Mulinia is a rather transient species, appearing sporadically and colonizing parts of the seafloor recently disturbed by bottom current scour or dredge spoiling.

showed high rates of growth and mortality, to (b) populations at high tidal level, barnacle encrusted areas in which growth and mortality were low, and where annual spawning represented a small percentage of the standing crop. Many populations studied correlated well with this tidal level pattern. However, it was also found that presence or absence of Balanus balanoides and/or Mytilus edulis could locally reverse population attributes based solely on the position of a population with respect to tidal level (Lewis and Bowman 1975).

As a final example, Brush (1974) derived population attributes for Mulinia lateralis, a filter-feeding mactid, and Nucula annulata, a deposit-feeding nuculid, for several areas in central Long Island Sound. One area considered was a dump site for dredge spoils from New Haven Harbor. A second location several kilometers from this dump site, and thought to be relatively undisturbed for a long period of time, was also studied. In comparing samples from these two localities, Brush concluded that the opportunistic bivalve Mulinia showed higher abundances, growth rates, and survivorship at the dump site than at the undisturbed station. The k-selected species Nucula, showed the opposite trend. In view of the earlier discussion of the adaptive strategies of these two species, the spatial patterns in population attributes are exactly what one would expect.

To further interpret these patterns one needs, however, additional information. The dump site was similar to the undisturbed station in sediment type. Both areas had a silt-clay substratum (Rhoads et al. 1975). The undisturbed area was dominated by a deposit-feeding community (Rhoads and Michael 1974). The sediment was highly bioturbated, uncompacted, and the bottom was frequently resuspended by tidal scour (Rhoads et al. 1975). Bottom resuspension would result in burial of juvenile M. lateralis and interfere with filter-feeding mechanisms (Rhoads and Young 1970; Levinton and Bambach 1969). The poor growth and survivorship of Mulinia at this station may, therefore, have been due to the presence of a well developed deposit-feeding community. This phenomenon is known as trophic group amensalism (Rhoads and Young 1970). On the other hand, the dump site had a dense population of opportunistic tubicolous polychaetes. These dense tube aggregations may have bound the sediment surface and prevented erosion or resuspension (Brush 1974). Mulinia, as a filter-feeder, would therefore be expected to do better on such a firm bottom where it was not competing with deposit-feeders.

In conclusion, trends in population attributes can be used to infer spatial and temporal gradients in ecological stress. Relating these trends to specific environmental factors may, however, require supplementary biological information. If the species chosen for study are carefully selected, most problems with interpretation could, I believe, be resolved. Molluscs are an ecologically diverse group ranging in adaptive types from opportunists to equilibrium species. They are found in epifaunal, infaunal, and pelagic habitats and represent a wide range of reproductive, dispersal, and feeding types. The potential for assessing environmental change through class-frequency analysis of molluscan populations is, therefore, very high.

In only a year or two, a population may appear in an area, reach very high densities, and then experience catastrophic mortality (Levinton 1970; Levinton and Bambach 1969). Large populations of Nucula, however, tend to be more stable in time. Using such indicator species, it is possible to identify areas of local disturbance (Johnson 1972; McCall 1975).

V. POPULATION RESPONSES TO ENVIRONMENTAL STRESS

In general, the population attributes of shallow water molluscan species can be related to many environmental factors, including food supply, salinity, temperature, oxygen tension, water movement and turbidity, substratum composition and physical stability of the bottom, population density (both intra- and interspecific interactions), and the presence and concentration of chemical pollutants (Hallam 1965; Kinne 1970; Moore 1962; Hedgpeth 1963). The utility of population attributes to deduce environmental change is related to the degree of resolution afforded by class-frequency histograms, and how specific the environmental effect is on a population. For example, reconsider the age structure of the bivalve Spisula solida (Figure 4). The age structure suggests an environmental effect of probably short duration, because subsequent recruitment classes do not appear to have been affected.

In many instances, temporal and spatial trends in population attributes can be identified rather easily. For example, Barnes (1973) studied intertidal populations of the bivalve Cerastoderma edule from Southampton Water during 1971 (Figure 31). The observed trends (Figure 32) ranged from (a) populations near the head of the water markedly influenced by annual recruitment, and comprised mostly of young individuals, to (b) populations at the mouth little affected by year-to-year recruitment, and dominated by older individuals (Barnes 1973). The Cracknore Hard location (Figure 32g) was an exception to the described pattern. At this site the population was stable and was probably composed of one or two older age classes showing little growth during the year; recruitment was insignificant (Barnes 1973). The population at this location is probably an example of the "dominant age class" phenomenon discussed earlier.

In many cases, trends in population attributes can be related to environmental gradients as shown, for example, in the study of Cardium edule (Figure 33). In other instances, the source of environmental stress may not be easily recognized. Complex interactions between environmental factors are sometimes difficult to resolve without additional information on the biology of the species being studied. For example, Orton and Lewis (1931) correlated increased mortality in oyster drills (Murex erinaceus and Thais lapillus) with temperatures 2-6° C. below normal. Temperature, however, was not the direct cause of mortality. Increased mortality at low temperatures was due to the inability of the organisms to tolerate salinities which, at normal temperatures, were within their tolerance range (Moore 1958).

In a second example, Lewis and Bowman (1975) studied variations in recruitment, growth, and mortality in intertidal populations of the limpet Patella vulgata (Figure 34). Trends ranged from (a) populations at low tidal level on bare rock that were greatly influenced by annual recruitment, and

ACKNOWLEDGMENTS

The preparation of this chapter was made possible through support of the Environmental Protection Agency, Environmental Research Laboratory, Narragansett, Rhode Island (grant, R804-909-010).

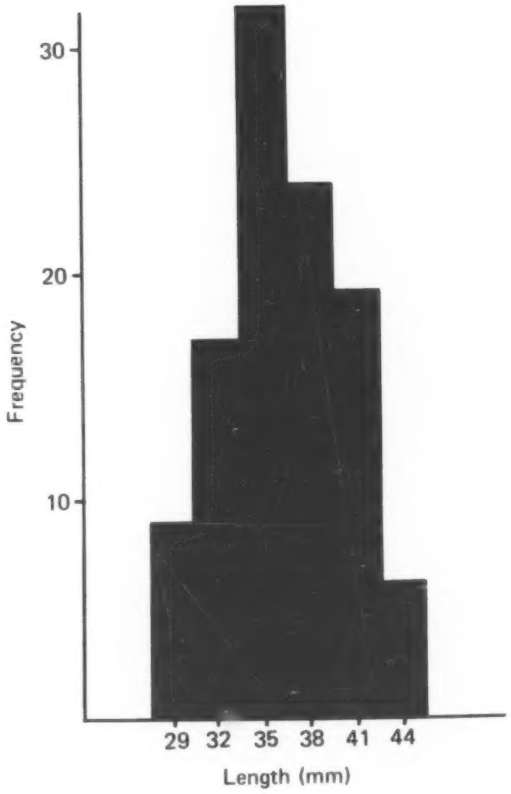
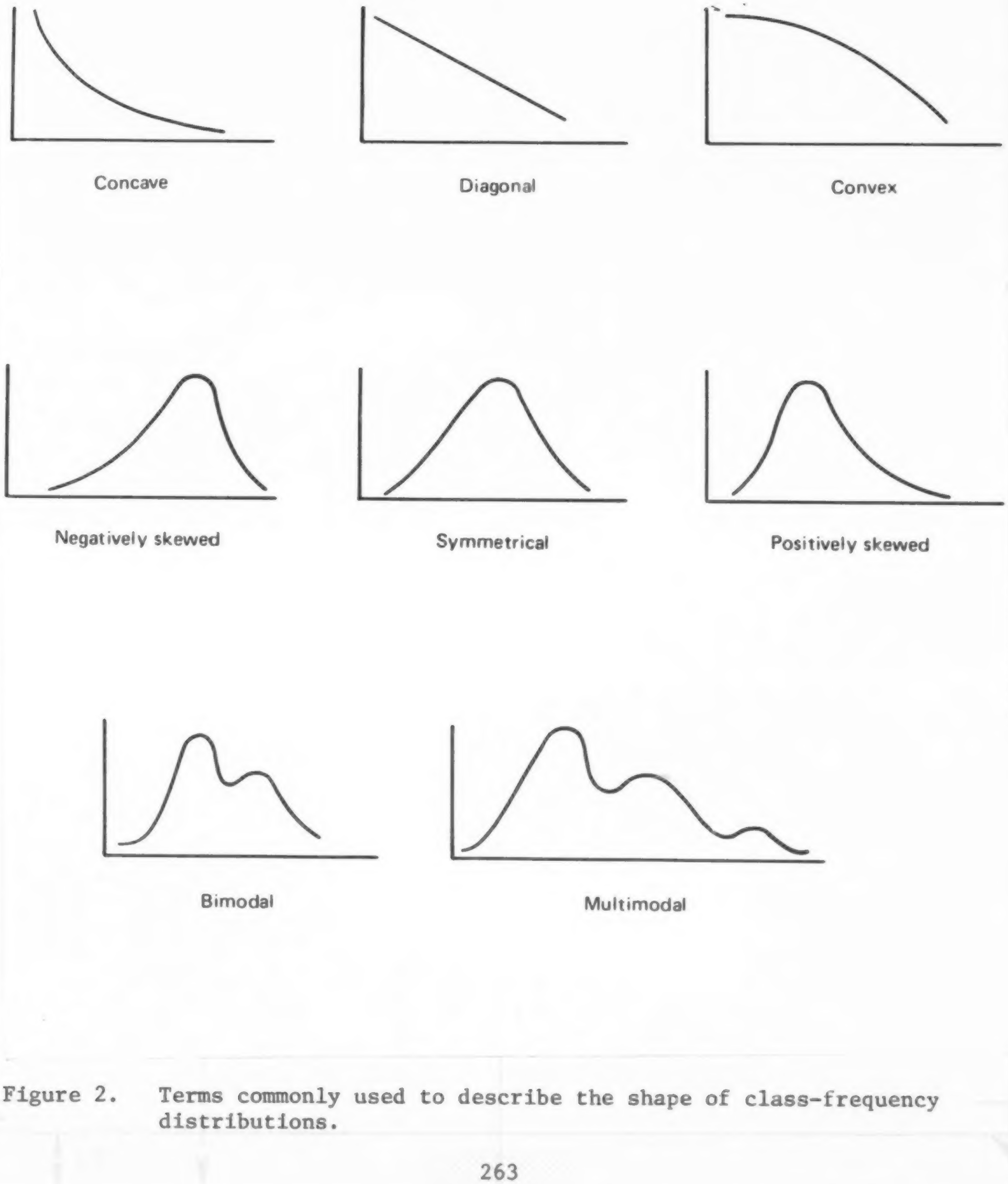


Figure 1. An example of a class-frequency histogram. Data from Table 1.



Concave

Diagonal

Convex

Negatively skewed

Symmetrical

Positively skewed

Bimodal

Multimodal

Figure 2. Terms commonly used to describe the shape of class-frequency distributions.

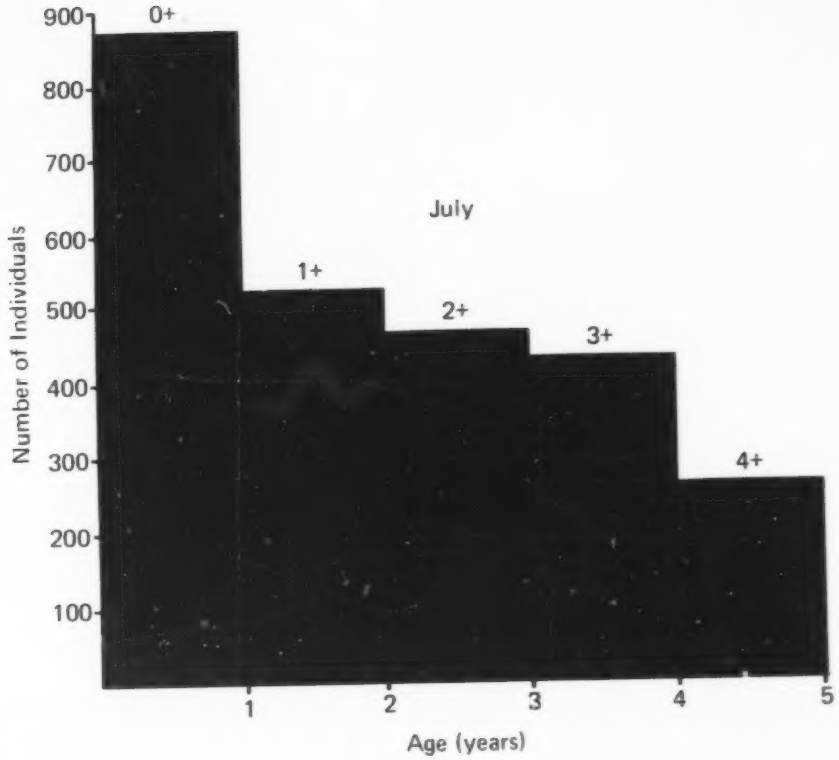


Figure 3. (a) A hypothetical sedentary population showing the effects of mortality on age structure. In this example, it is assumed that recruitment and mortality do not vary from year to year. Note mortality effects both within and between age classes. (a) The population as it might appear in July, just after annual spat fall. (b) The population as it might appear in January. No recruitment has taken place during the intervening period.

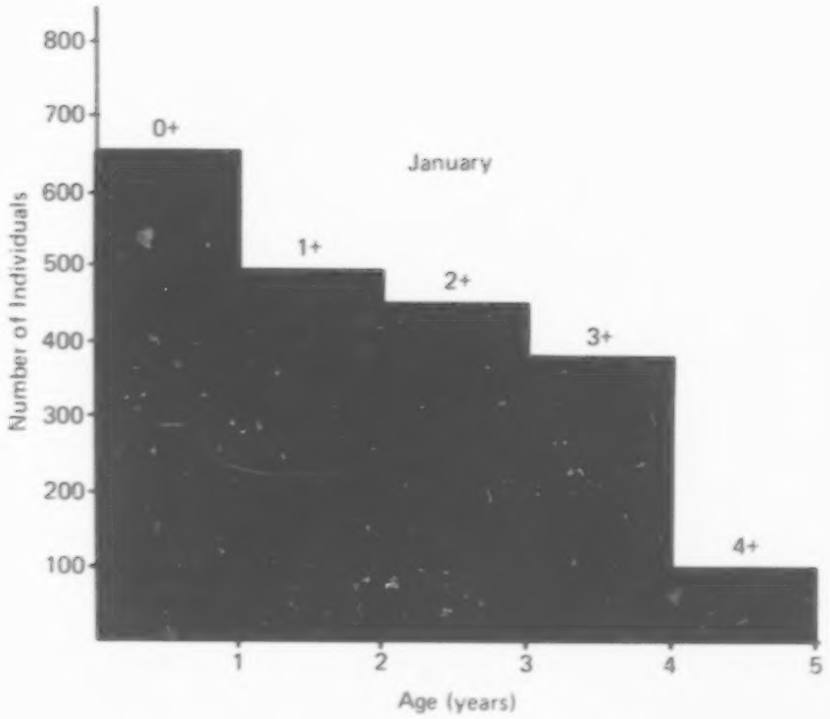

800
700
600
500
400
300
200
100
Number of Individuals
0+
January
1+
2+
3+
4+
1
2
3
4
5
Age (years)

Fig. 3(b).

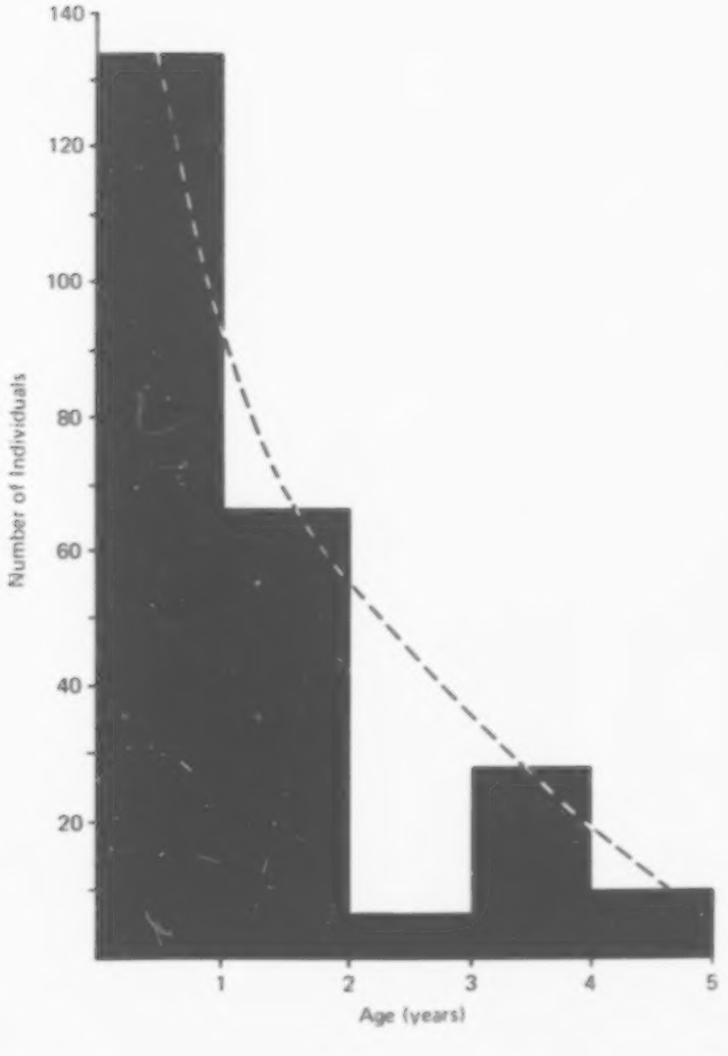


Figure 4. Age-frequency histogram of Spisula solida collected in 1972. Notice the weak representation of the 2+ year class. This is probably due to poor recruitment during 1970. Data estimated from Smith (1974).

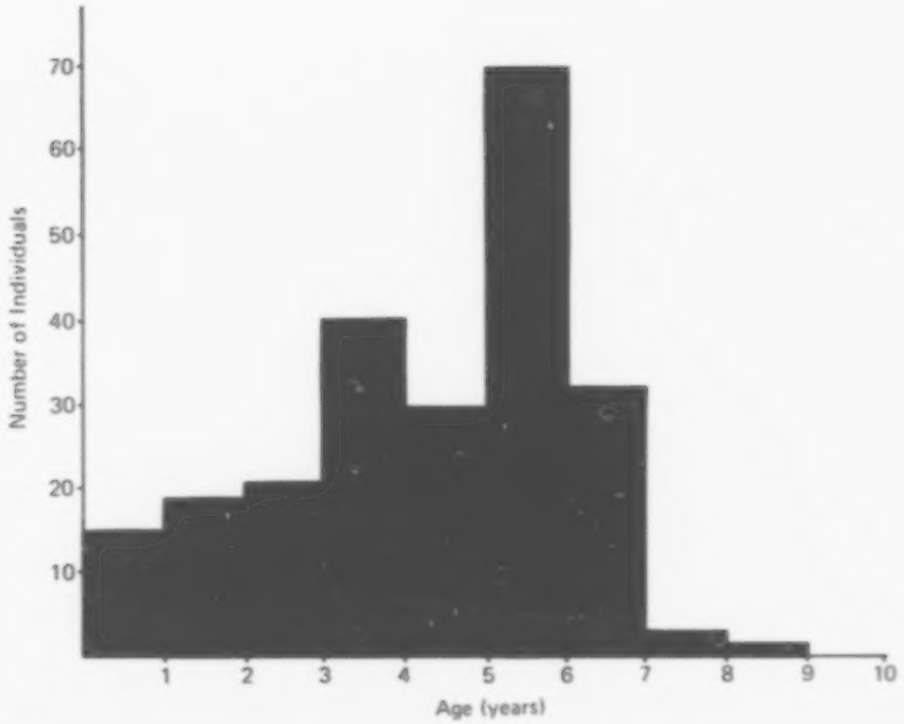


Figure 5. Age-frequency histogram of Venerepis pullastra. Note the numerical dominance of the older age classes (especially the 5+ year class). This particular age structure may be an example of the dominant age class phenomenon described in the text. After Johannessen (1973).

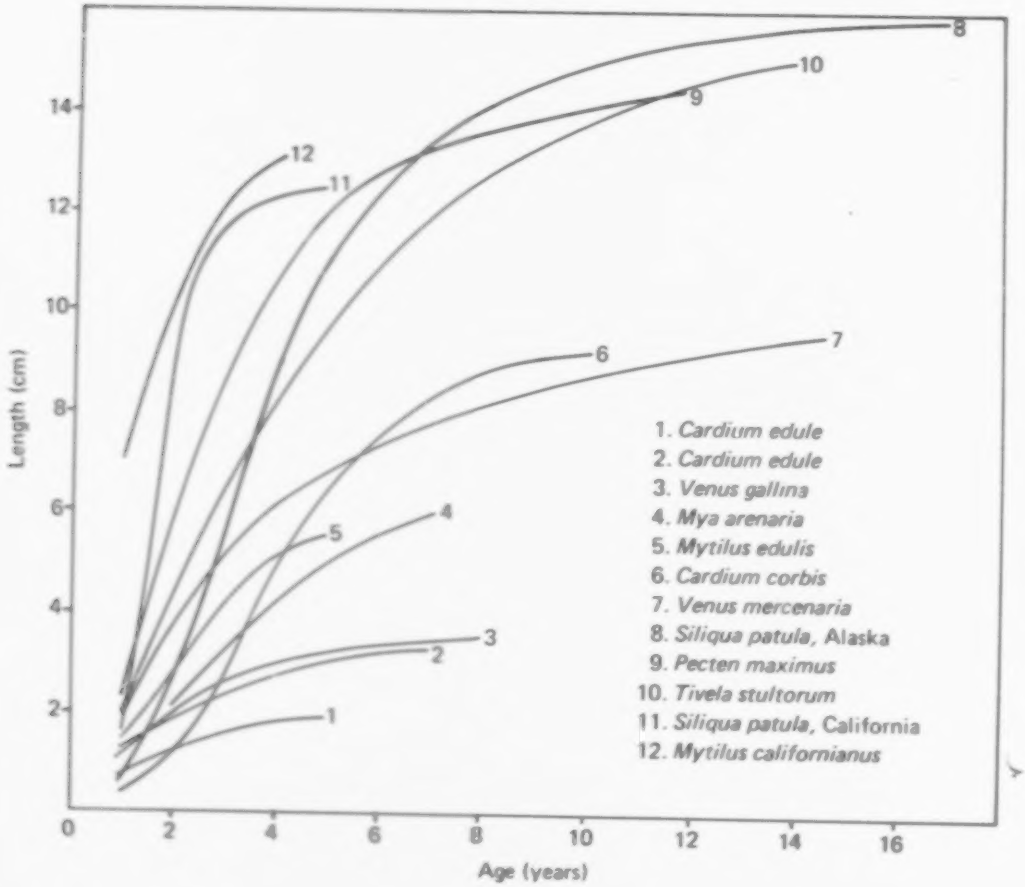


Figure 6. Growth curves for twelve species of bivalves. After Hallam (1967), who cites original sources.

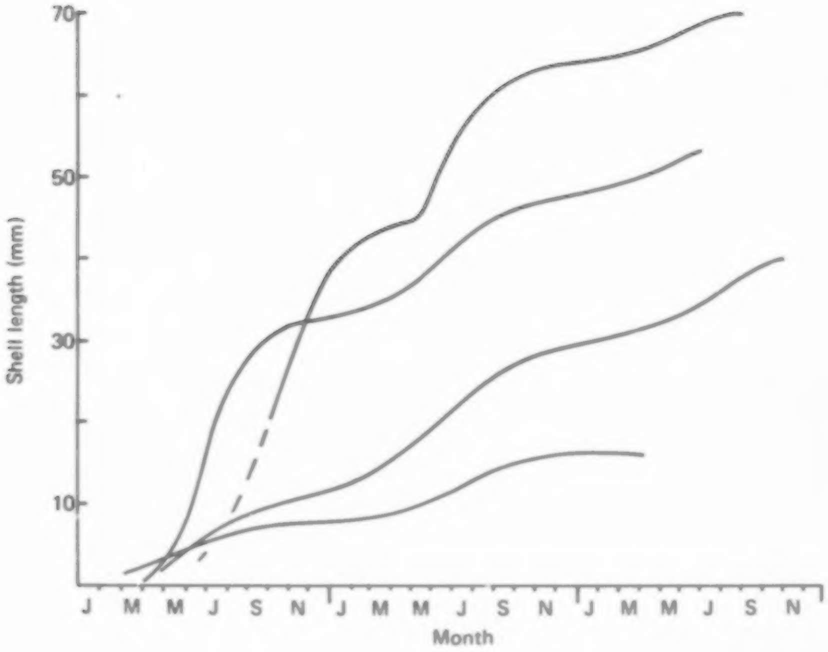


Figure 7. Temporal and spatial variations in growth for four populations of *Mytilus edulis*. After Seed (1976).

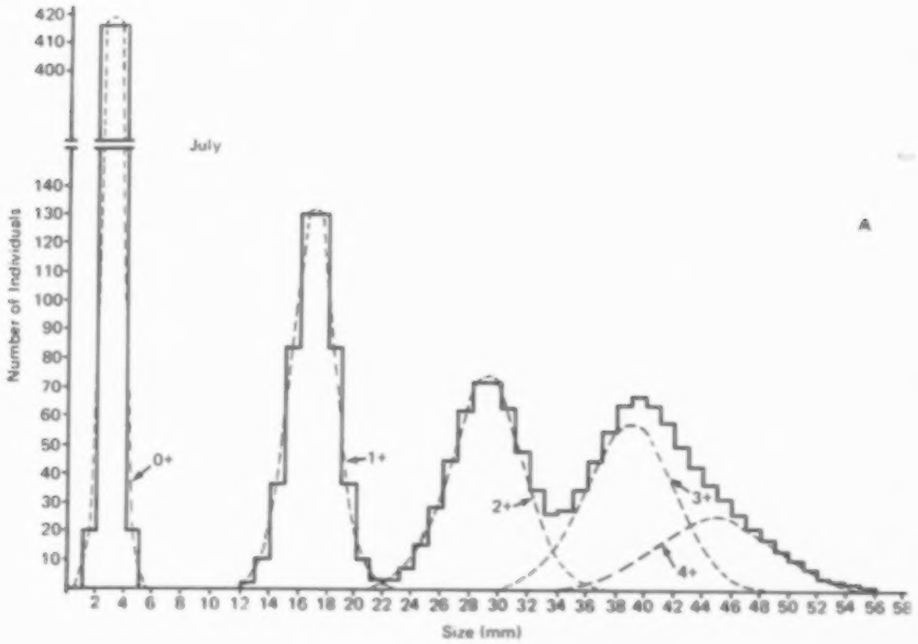


Figure 8. (a) A hypothetical example of the general form of size-frequency histograms for a molluscan population. Dotted lines represent individual recruitment classes. Notice the increased dispersion in size with age. Note also the overlap of the older age-classes. The histograms in this figure have the same age structure as the hypothetical population in Figure 3. (a) The population as it might appear in July. (b) The population as it might appear in January. Note that the modes in (b) are displaced to the right of those in (a) as a result of six months' growth.

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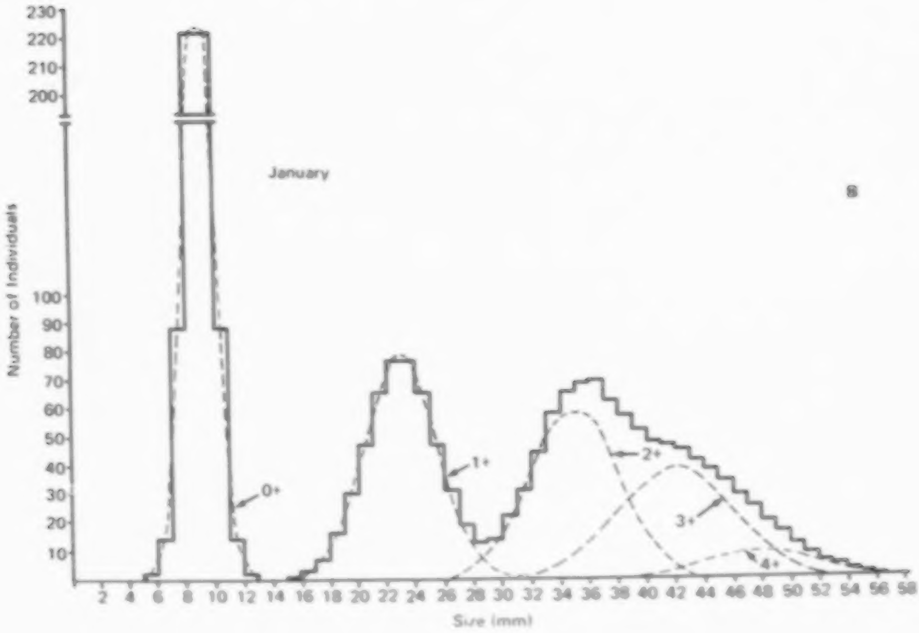

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Figure 8(b)

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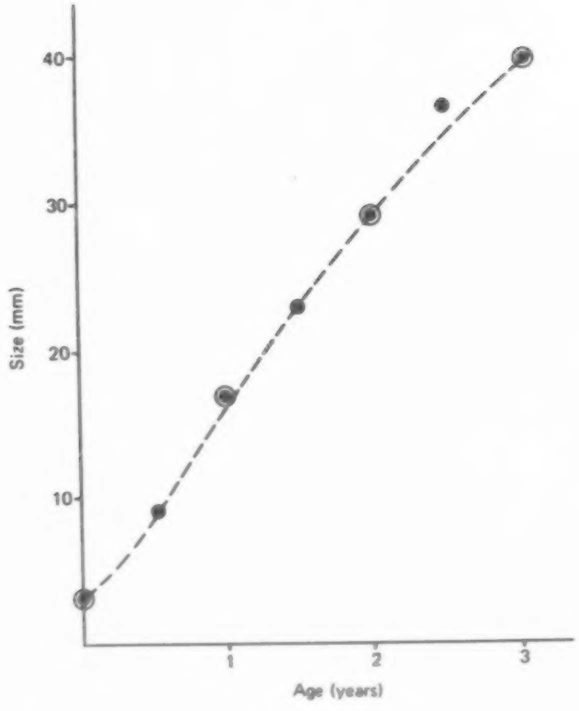

Figure 9. Growth curve constructed from the example in Figure 8 by plotting estimates of size for each discernible mode. The open circles represent points taken from the July histogram, and the closed circles are from the January histogram. Note that some of the older age classes are not represented.

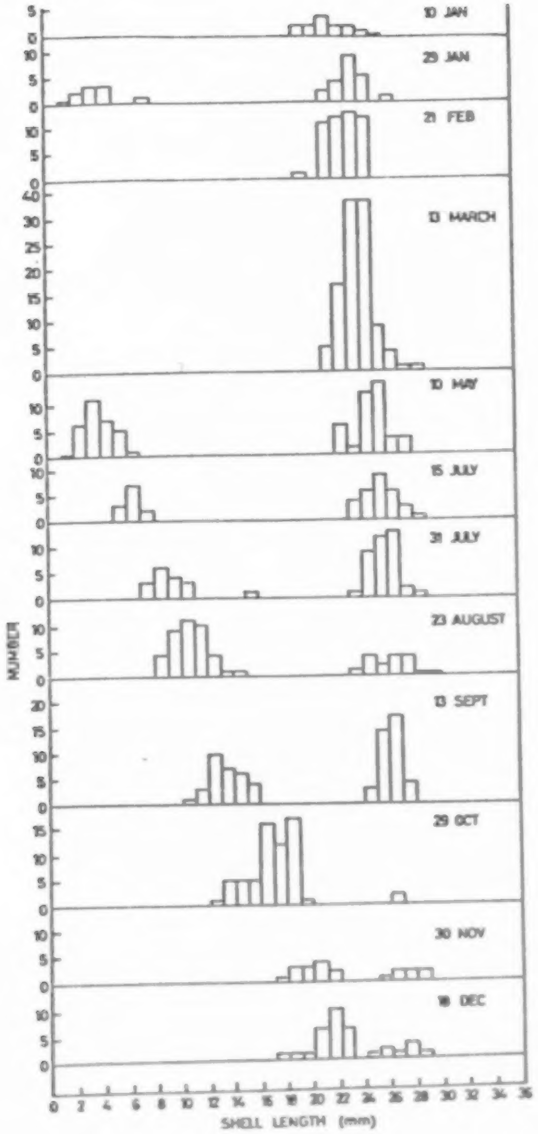

Figure 10. Size-frequency histograms of Donax incarnatus from Shertallai beach in 1968. Two year classes representing the 1967 and 1968 spatfalls are present in these samples. Note the displacement of modes to the right in this series due to growth. After Ansell, et al. (1972).

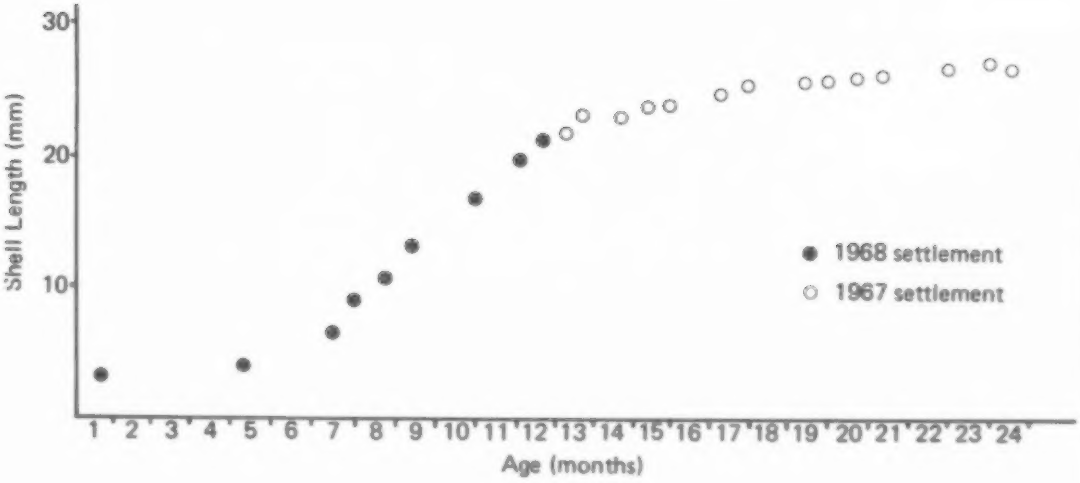

Figure 11. Growth curve for Donax incarnatus derived by plotting mean shell lengths in Figure 10 as a function of time. After Ansell et al. (1972).

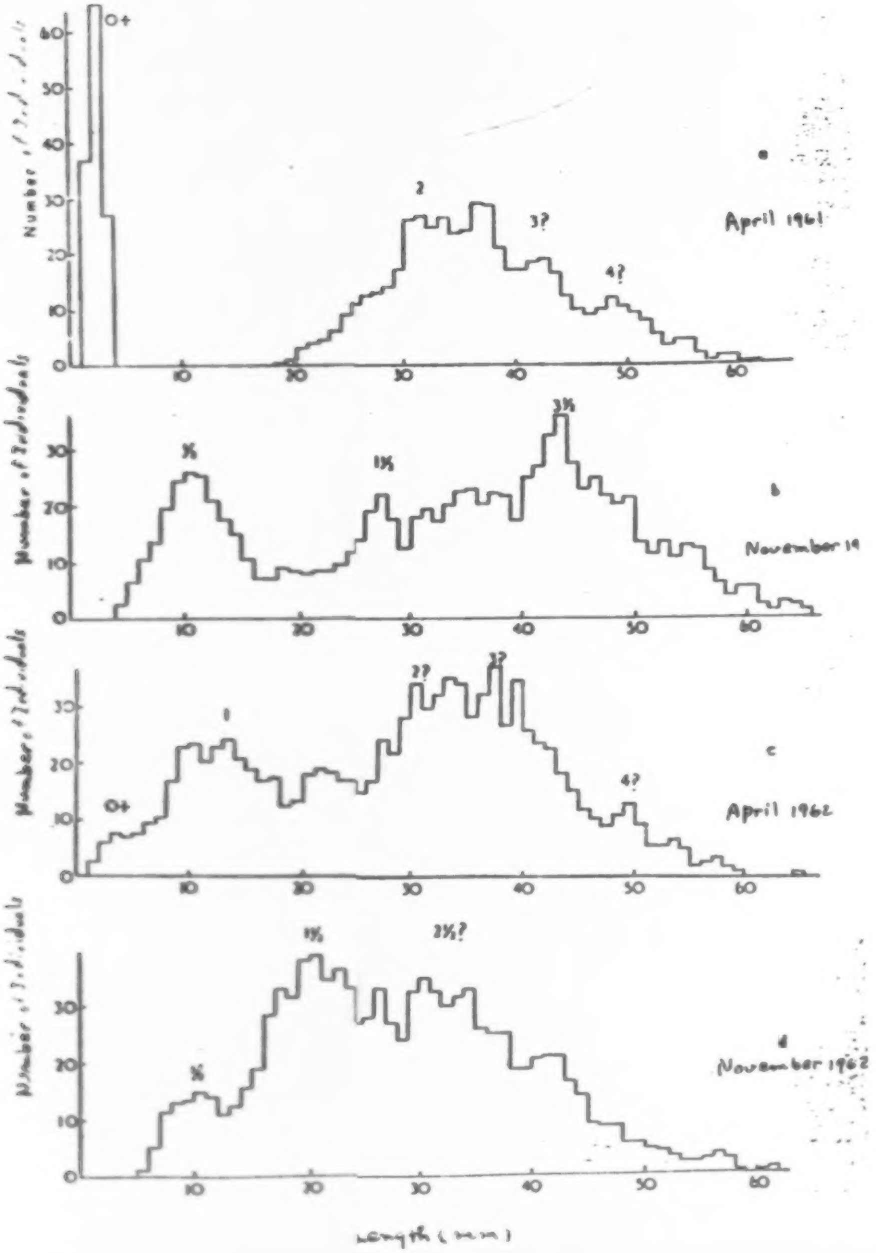

Figure 12. Size-frequency histograms of Mytilus edulis from Ferny Ness, East Lothian. Sampling dates are given. Age-class assignments shown were determined by Craig and Hallam (1963) on the basis of mode identification and growth information (Figure 13) reported by Savage (1956). After Craig and Hallam (1963).

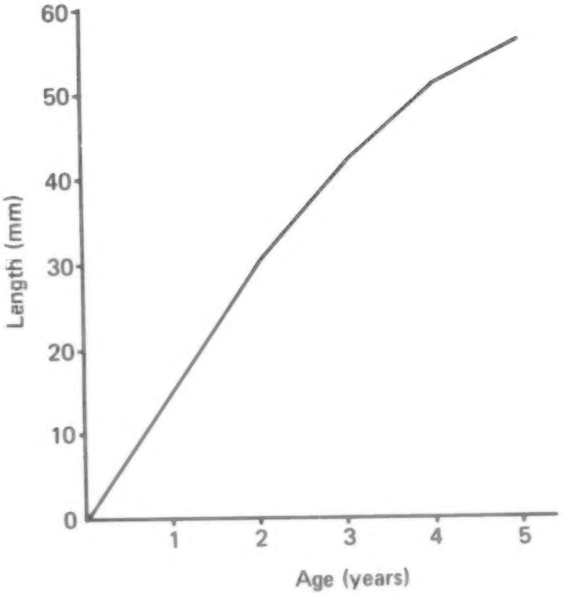

Figure 13. Growth curve derived for *Mytilus edulis* from data provided by Savage (1956). This growth data was used by Craig and Hallam (1963) to assign age-classes in Figure 12. After Craig and Hallam (1963).

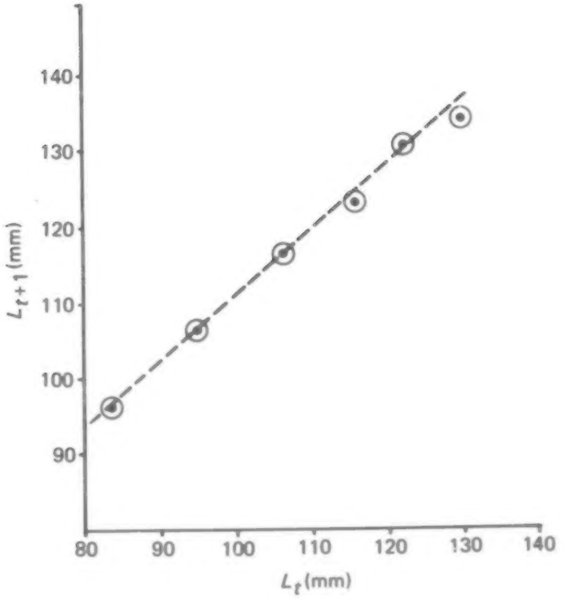

Figure 14. Walford plot for Placopecten magellanicus derived from length at age data collected by Merrill et al. (1965). Note that the data plot is a straight line.

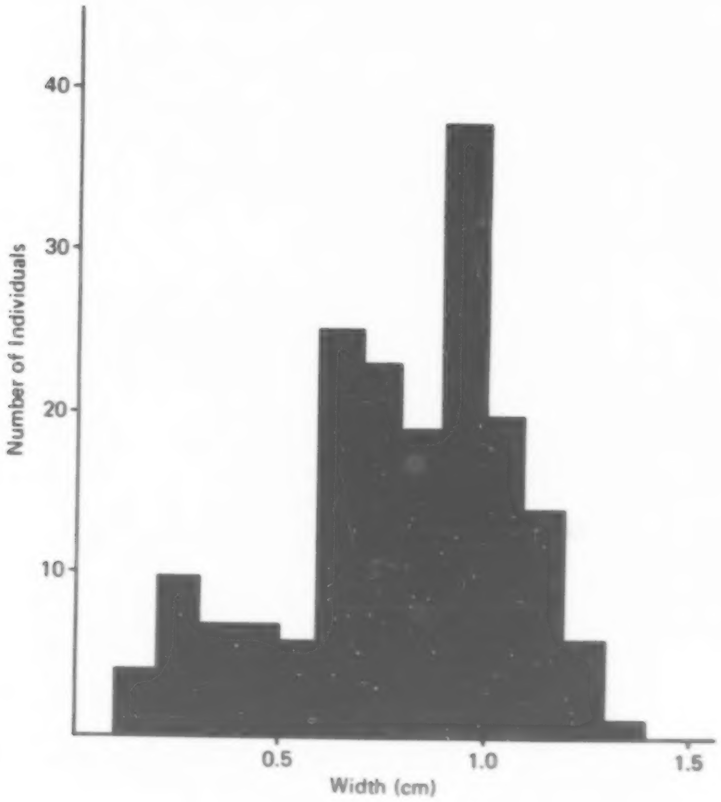

Figure 15. Size-frequency histogram of the fossil brachiopod Chonetes laguessiana. After Sheldon (1965).

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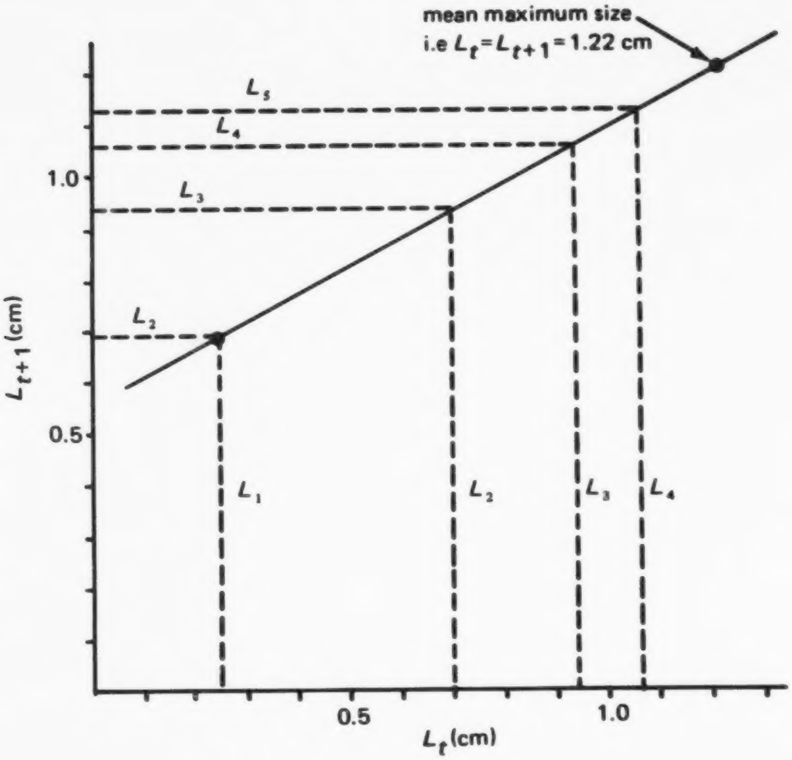

Figure 16. Walford plot for Chonetes laguessiana. Estimates of L_1, L_2, and the mean maximum size are from Figure 15. The Walford plot suggests that a mode representing the third year class should be located at 0.93 cm. In Figure 15 note that a mode is located at approximately the same position as predicted. After Sheldon (1965).

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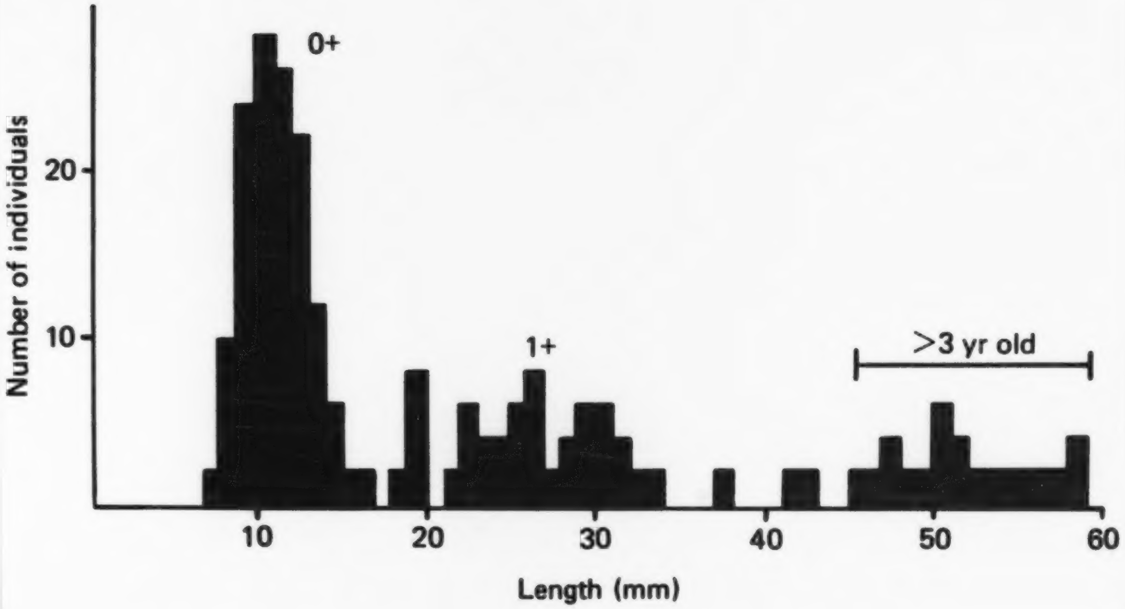

Figure 17. Size-frequency histogram of Spisula solida collected in 1972. The peaks at 12 and 27 mm represent the 0+ and 1+ year classes respectively. From the Walford plot in Figure 18, a peak representing the 2+ year class should have been located at 38 mm. The absence of this peak suggests poor recruitment during 1970. After Smith (1974).

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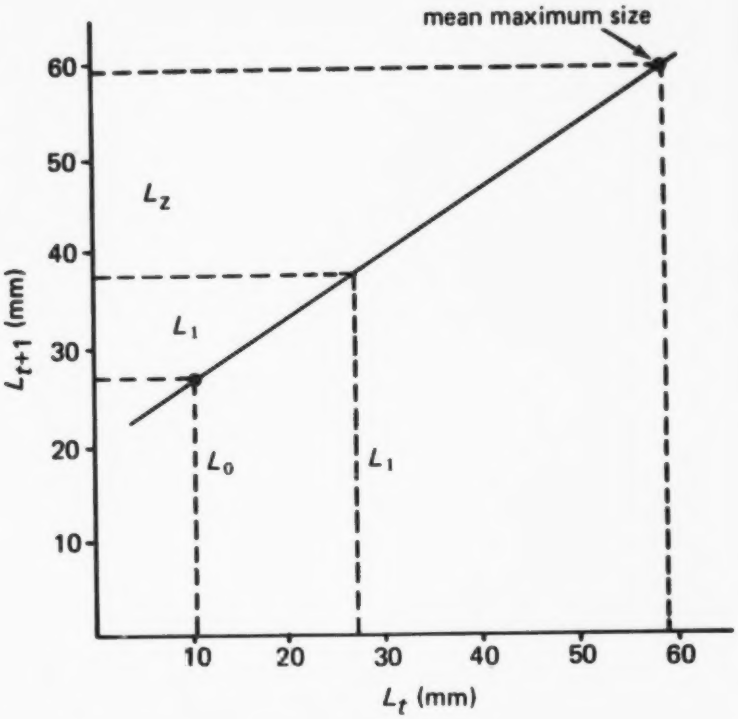

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Figure 18. Walford plot of Spisula solida. Data from Figure 17. The Walford plot predicts a peak in the size-frequency histogram at about 38 mm.

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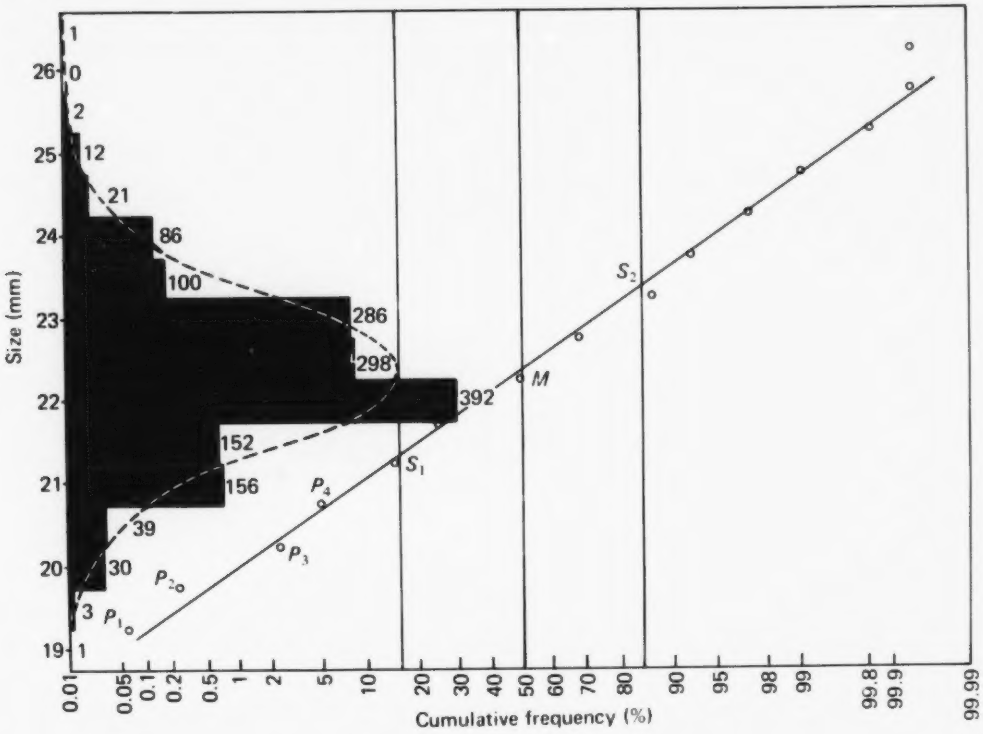

Figure 19. Size-frequency histogram of 1572 individual size measurements plotted as cumulative percentages on probability paper. The horizontal scale represents the cumulative percentage. The vertical scale is size in mm. Note that a normal distribution plots as a straight line on probability paper. After Harding (1949).

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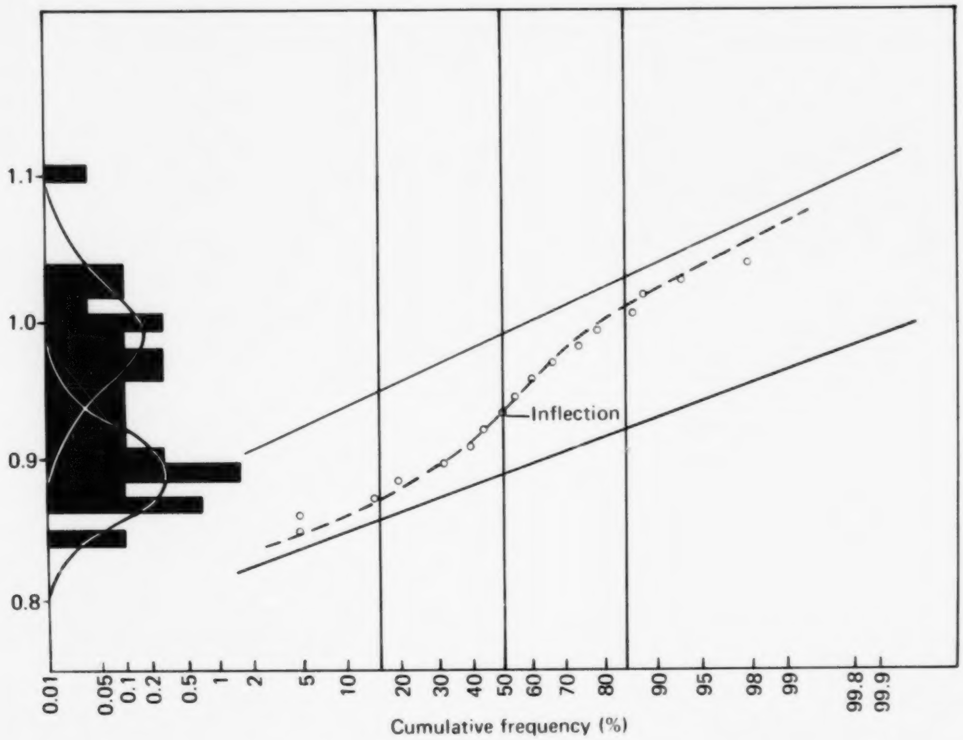

Figure 20. A plot on probability paper of two overlapping normal distributions. Note the single point of inflection at 50%. After Harding (1949).

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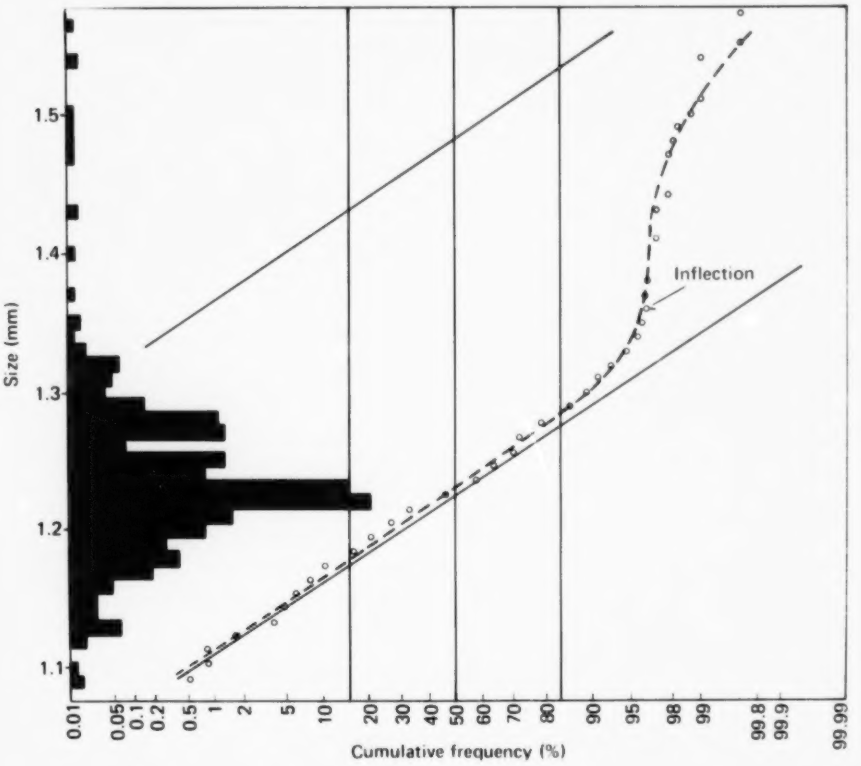

Figure 21. A plot on probability paper of two overlapping normal distributions. Note the single point of inflection at 97%. After Harding (1949).

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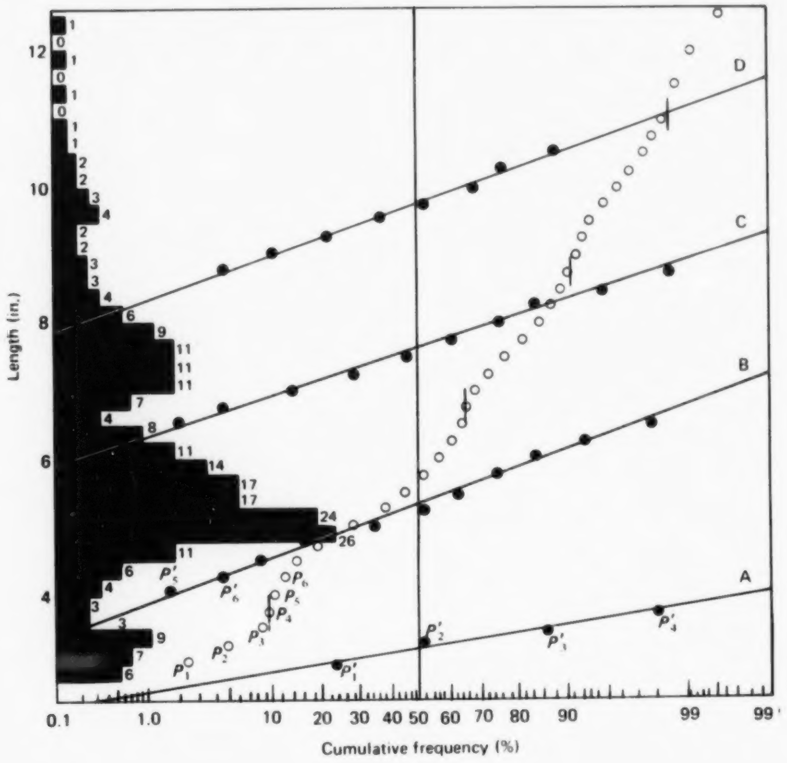

Figure 22. Size-frequency histogram of 256 measurements plotted as cumulative percentages on probability paper. Notice the four points of inflection. They imply that the population is made up of at least five overlapping normal distributions. Modified from Cassie (1954).

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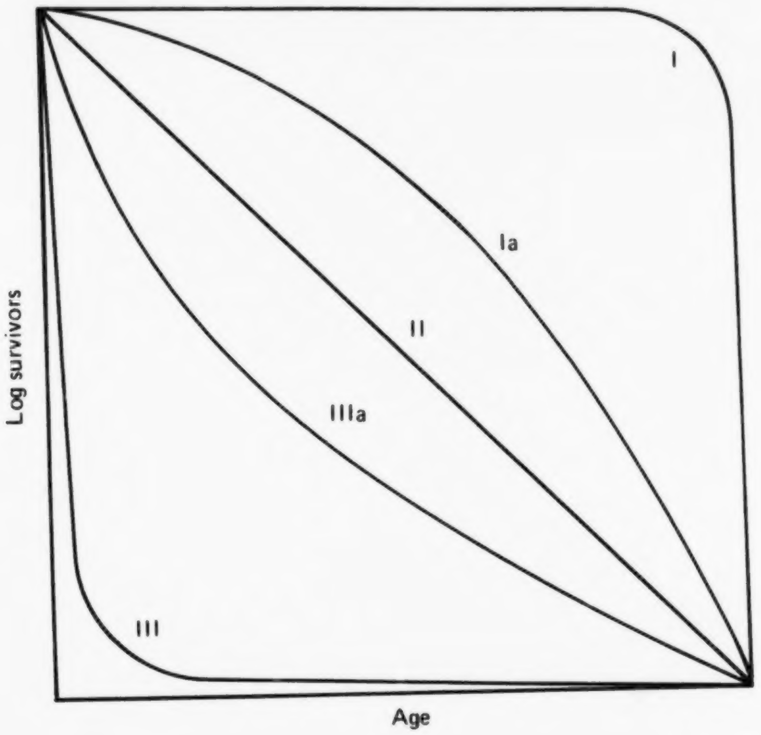

Figure 23. Theoretical survivorship curves. Type I: Low mortality early in life, but high mortality in old age. Type II: Constant mortality throughout life. Type III: High mortality early in life. Types Ia and IIIa are less extreme versions of I and III. From Deevey (1947).

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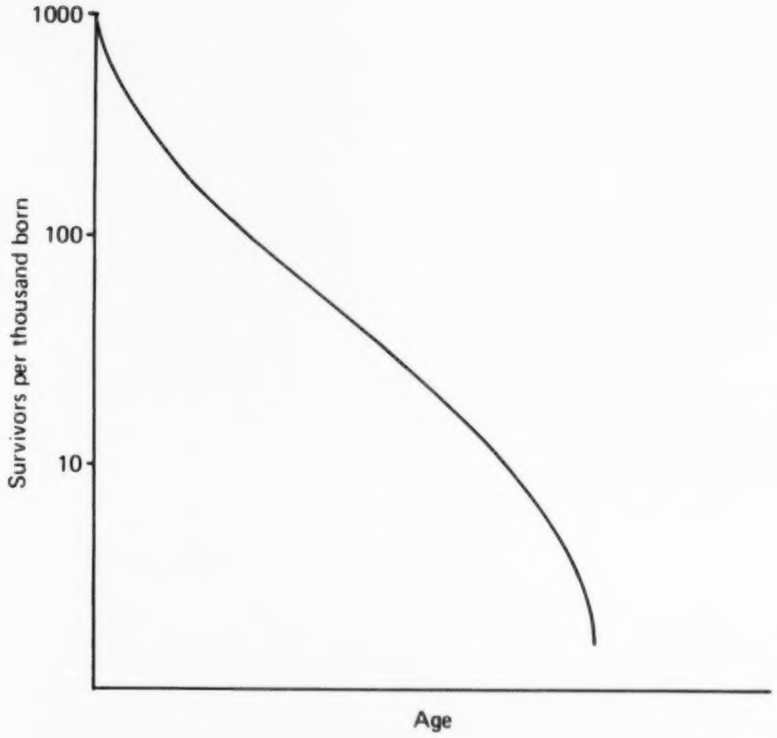

Figure 24. Hypothetical shape of a survivorship curve representative of a population in which a complete record is available, including all larval, juvenile, and adult stages. Suggested by Kurtén (1964).

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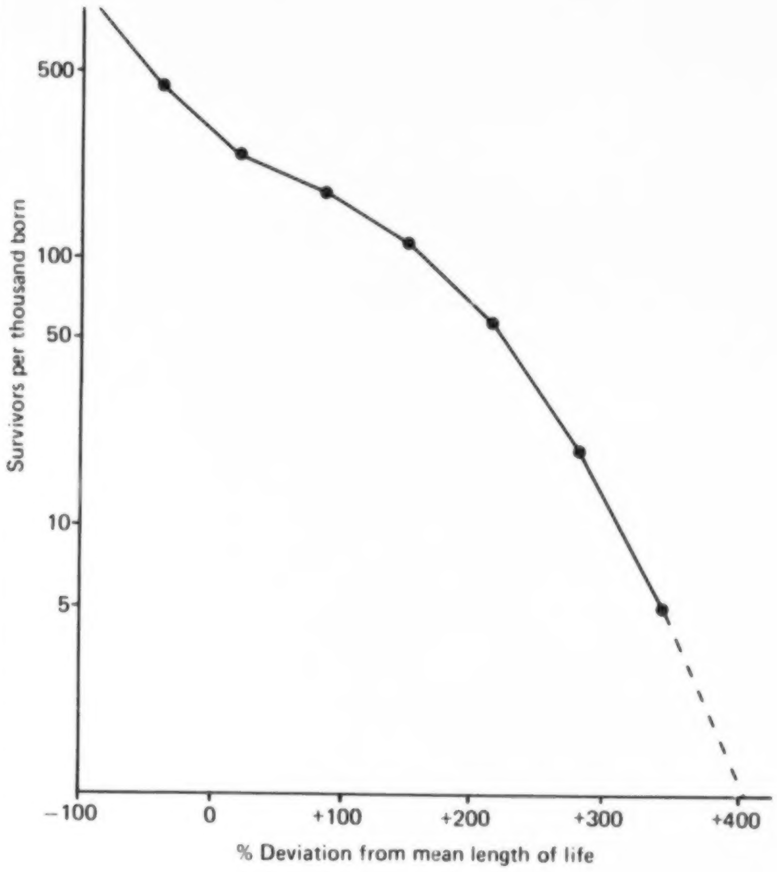

Figure 25. Survivorship curve for the California Pismo Clam, Tivela stultorum. Survivorship data from Table 2. Note the sigmoidal shape even though only post-larval individuals were used in the analysis.

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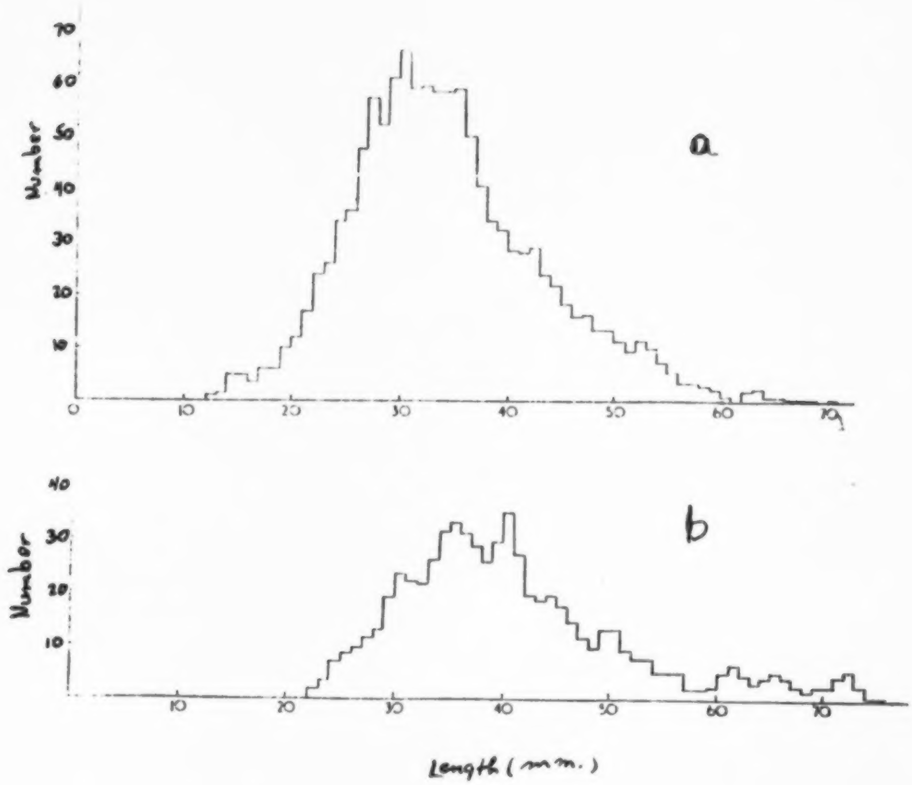

Figure 26. Survivorship curves for two populations of Mytilus edulis derived
(a & b) from death assemblages. (a) A valve assemblage from Ferny Ness. (b) A valve assemblage from Craigelaw Bay. (c) Survivorship curves computed from (a) and (b). Note the close similarity in survivorship. After Craig and Hallam (1963).

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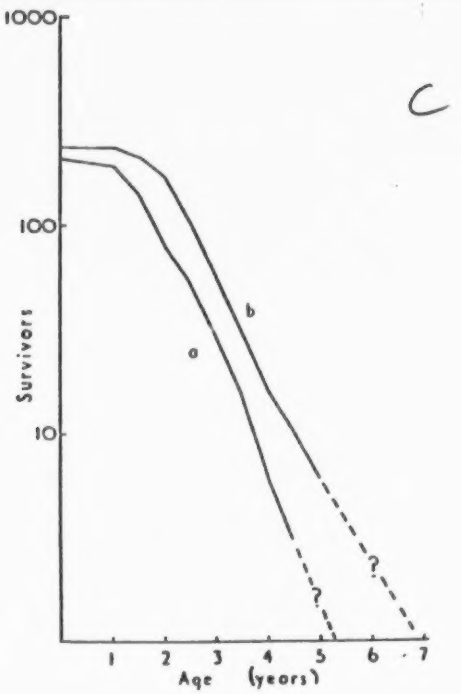

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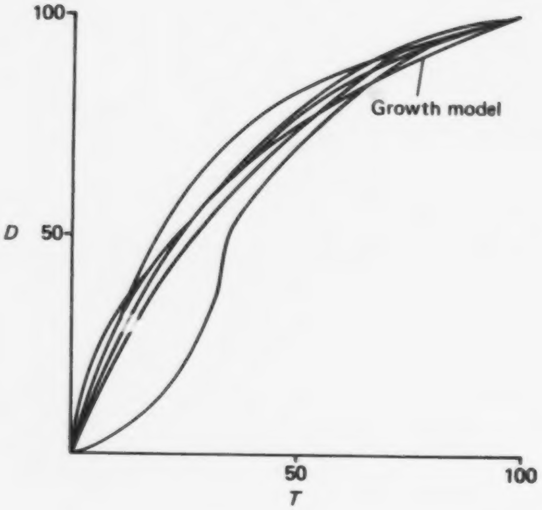

Figure 27. Fit of the growth model $D = s \ln(T+i)$ to five growth curves chosen at random from Hallam (1967). The growth curves may be found in Figure 6. In the model, D is the size, T is the relative age, and s is a constant. Both D and T in the figure are expressed as percentages. After Levinton and Bambach (1969).

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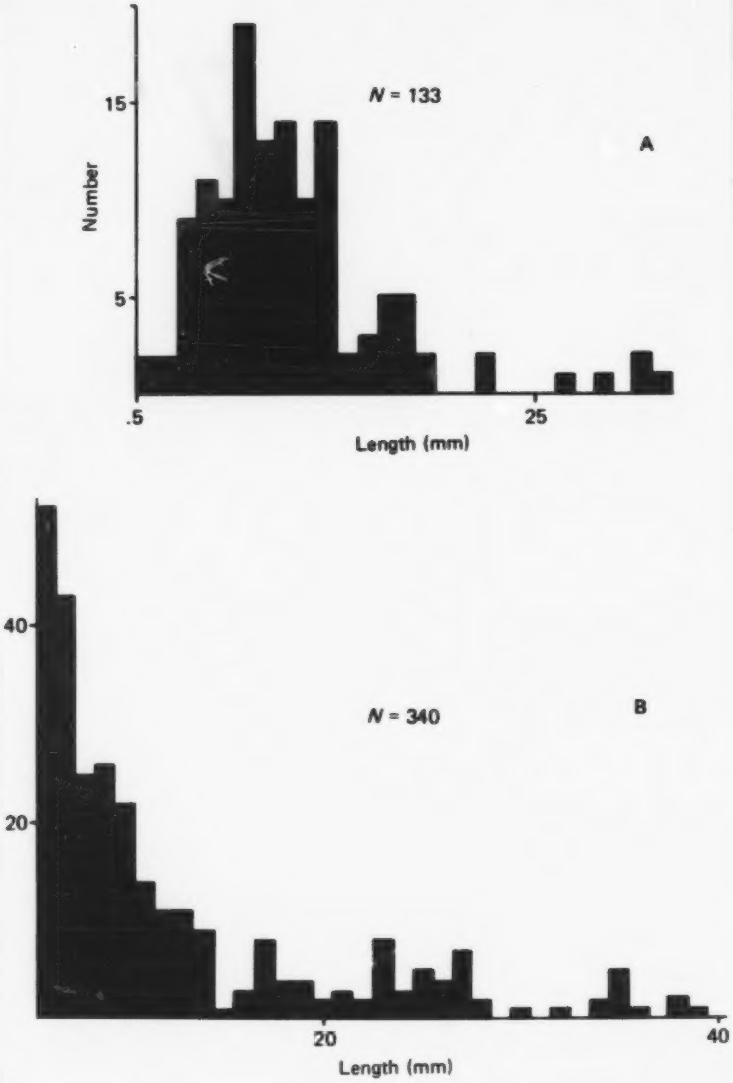

Figure 28. (a & b) Survivorship curves for two populations of Yoldia limatula derived from death assemblages. Both populations are from a shallow water mud habitat in Long Island Sound. (a) Size-frequency histogram of a death assemblage taken at a water depth of 7 m. (b) Size-frequency histogram of a death assemblage collected at a water depth of 20 m. This second area was characterized by a thin non-cohesive, mobile layer at the sediment-water interface. (c) Survivorship curves computed from (a) and (b). Note the relative time scale. Slightly higher juvenile mortality in (b) is attributed to poor physical support provided by the substrate. Lower size-classes in (a) and (b) excluded by sieving. After Levinton and Bambach (1969).

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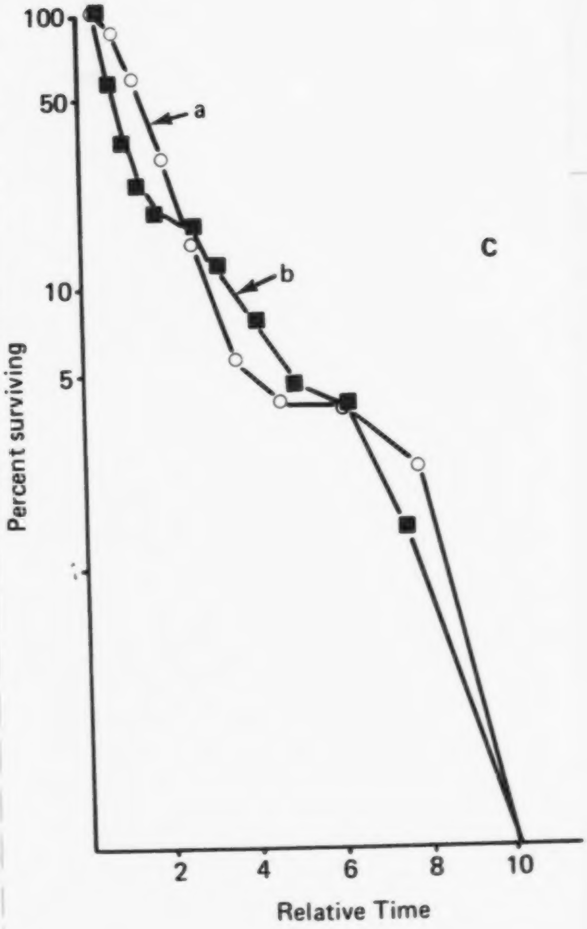

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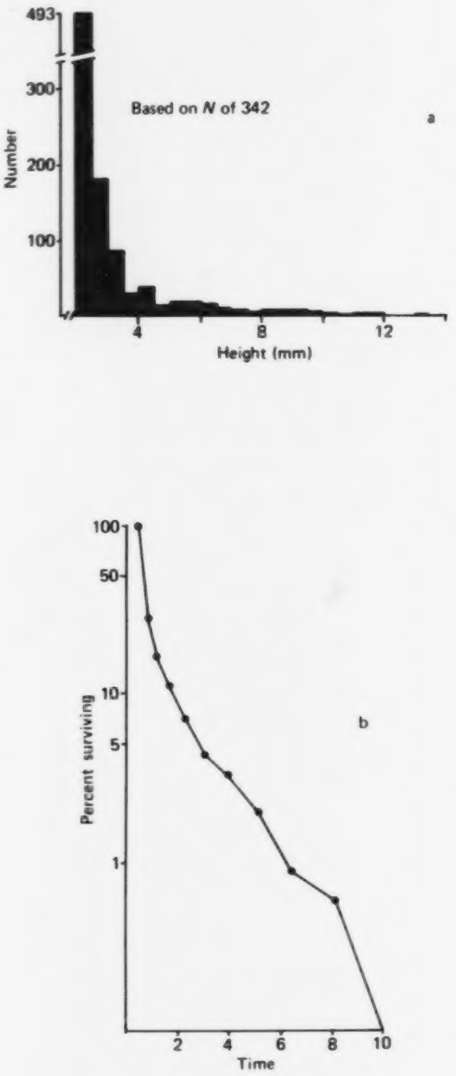


Figure 29. A survivorship curve for a population of Mulinia lateralis derived from a death assemblage. (a) Size-frequency histogram of a death assemblage collected in Long Island Sound. (b) Survivorship curve computed from (a). Note the relative time scale. Lower size-classes excluded by sieving. After Levinton and Bambach (1969).

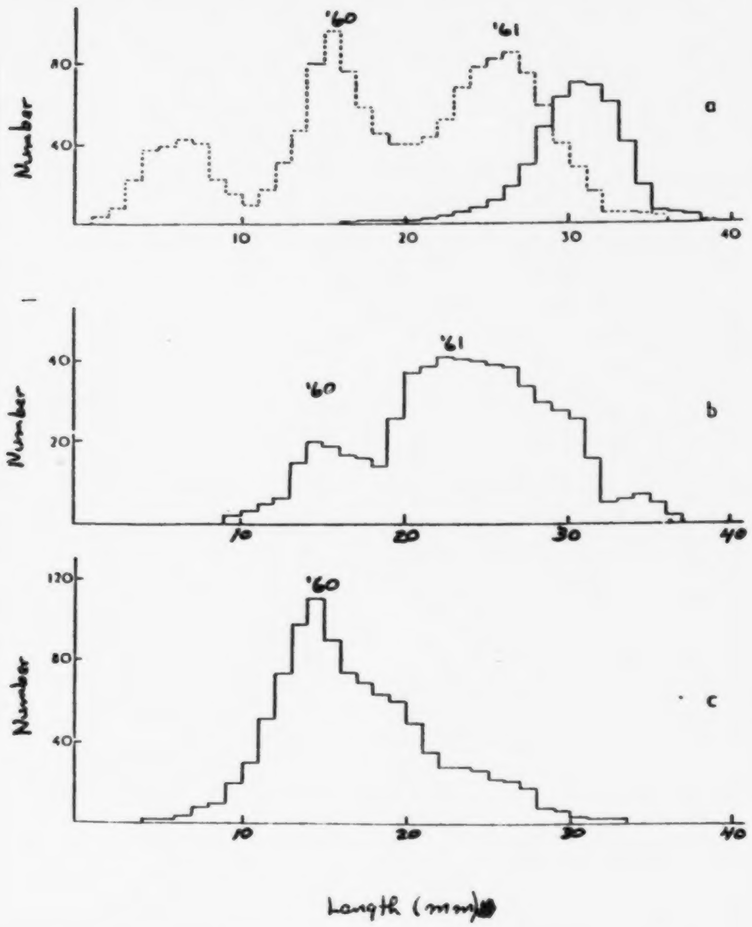
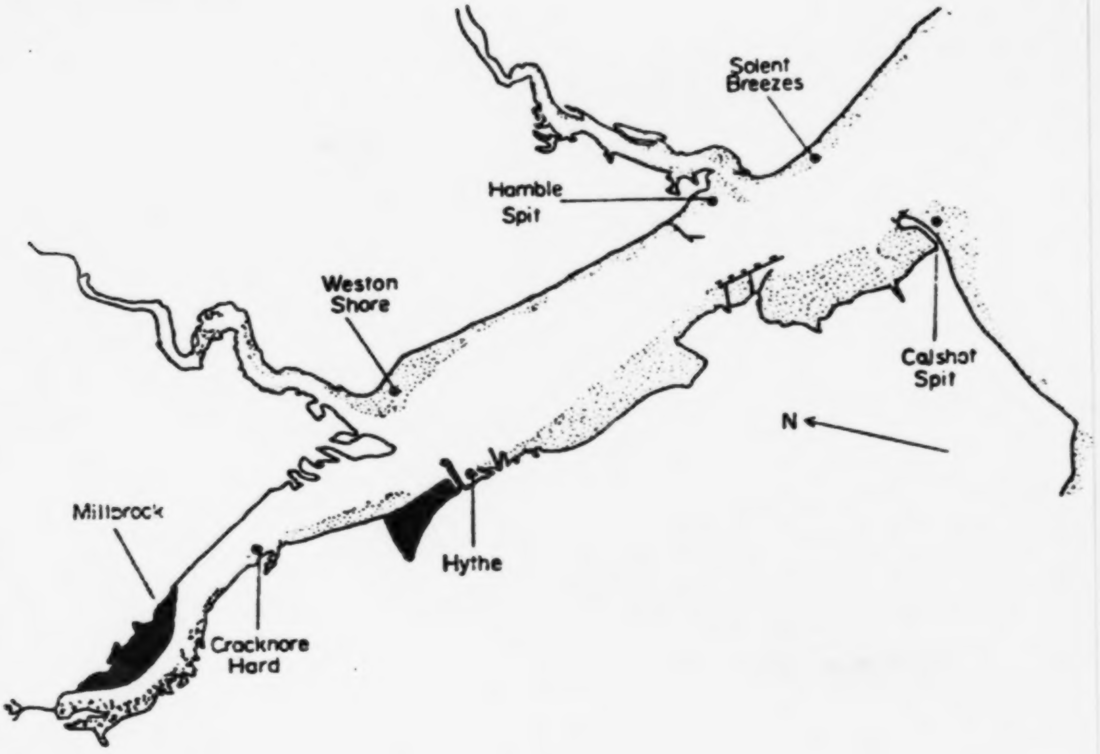


Figure 30. Size-frequency histograms of Cardium edule from Peffer Burn, East Lothian. This census was taken in May, 1962. (a) Solid lines represent the living population. Dotted lines are growth ring size-frequencies. The living population is unimodal and probably represents a single year-class. Two peaks in the growth ring size-frequency histogram correspond to the winters of 1960 and 1961. The smaller peak at 6.5 mm represents a growth ring which apparently developed shortly after spatfall in summer 1960. Because of shell abrasion in the umbonal region this growth ring was discernible on only part of the living population. (b) Articulated dead shells. Note the correlation between peaks in the growth ring size-frequency distribution and peaks in this death assemblage. Individuals dying in the most recent winter are represented to a large extent by articulated shells. (c) Disarticulated death assemblage (right valves only). Note the correlation between the peak here and the 1960 winter peak in the growth ring size-frequency histogram. After Craig and Hallam (1963).



igure 31. Sketch-map of Southampton Water. Population samples in Figure 32 were collected from the stations shown. The littoral zone is stippled, and the areas in the process of reclamation are shown blackened. After Barnes (1973).

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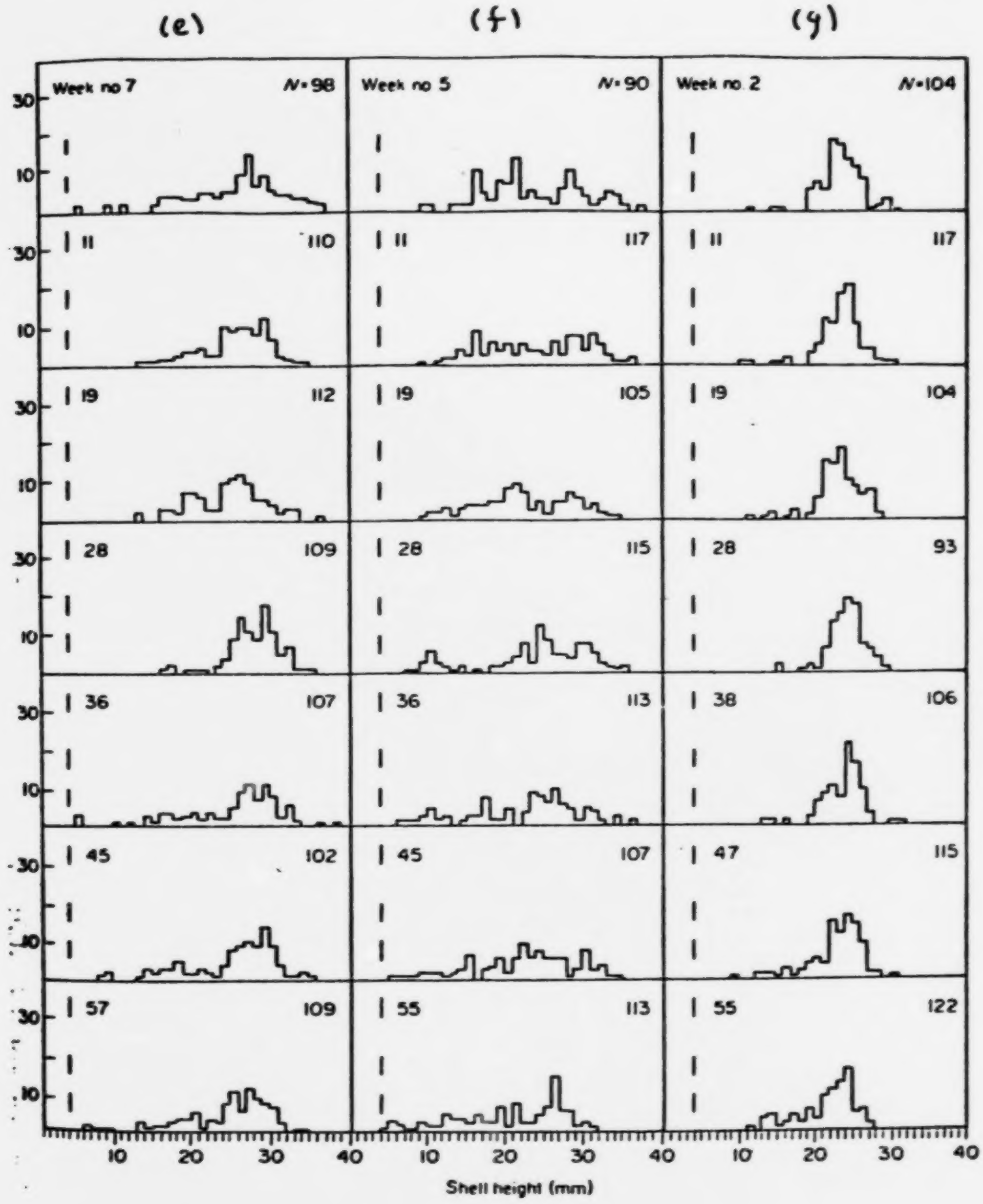

Fig. 32 (e, f & g)

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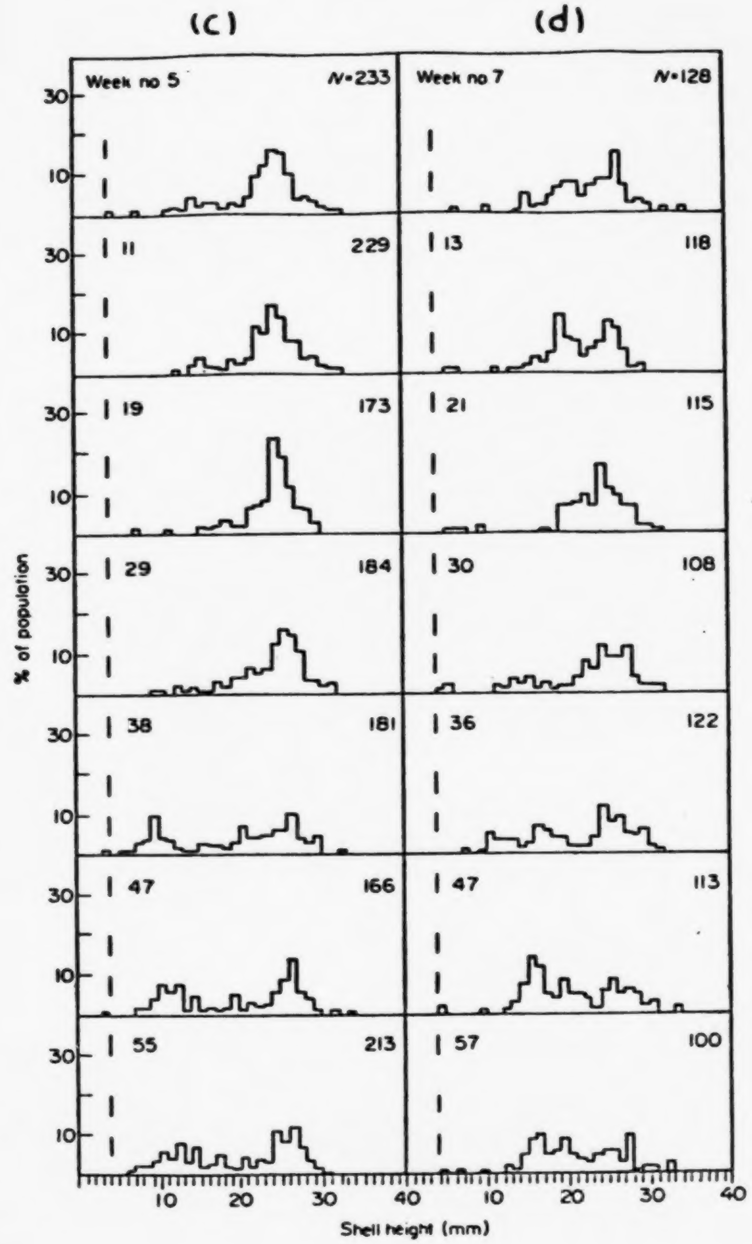

Fig. 32 (c & d)

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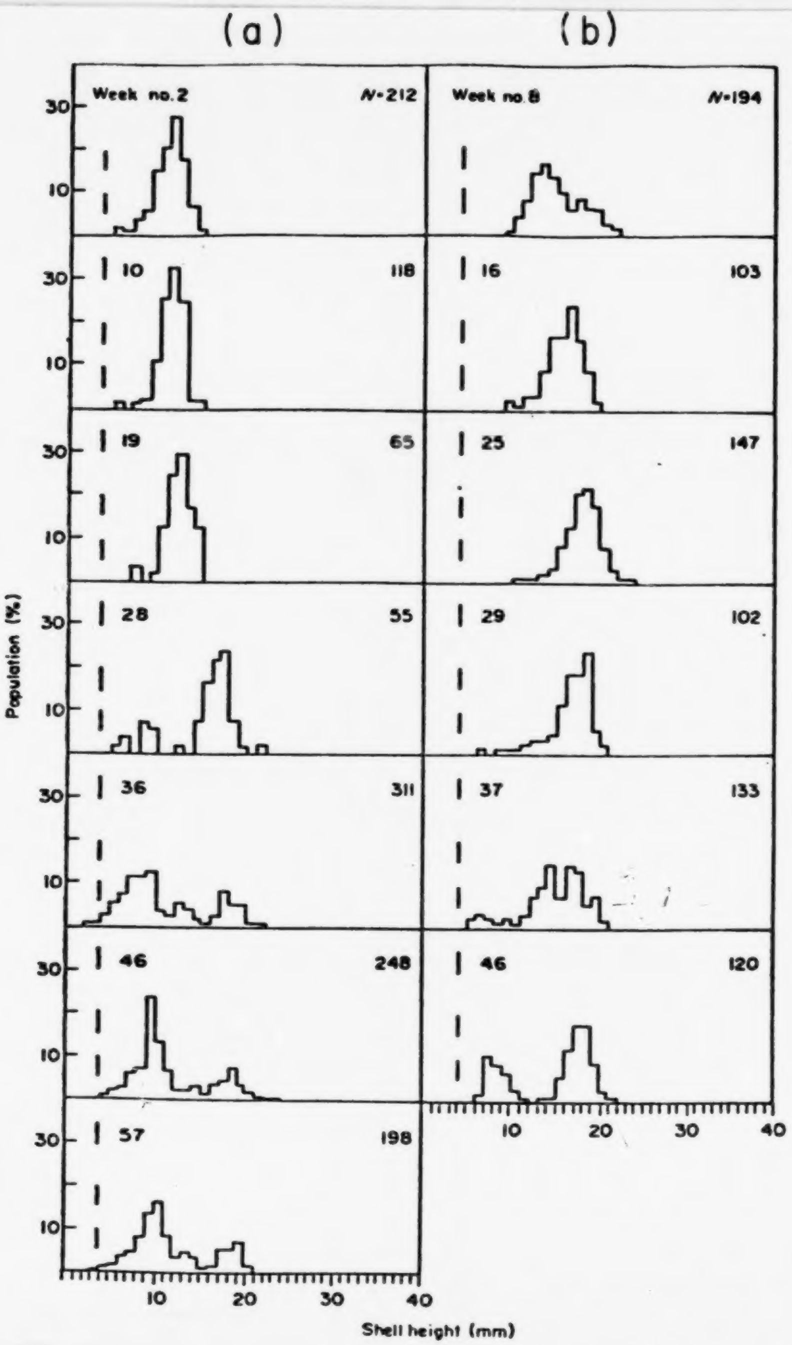

Figure 32. (a & b) Size-frequency histograms of Cerastoderma edule from Southampton Water during 1971. Collecting stations: (a) Hythe, (b) Millbrook, (c) Weston Shore, (d) Hamble Spit, (e) Solent Breezes, (f) Calshot Spit, and (g) Cracknore Hard. Note variations in recruitment and age structure between localities. After Barnes (1973).

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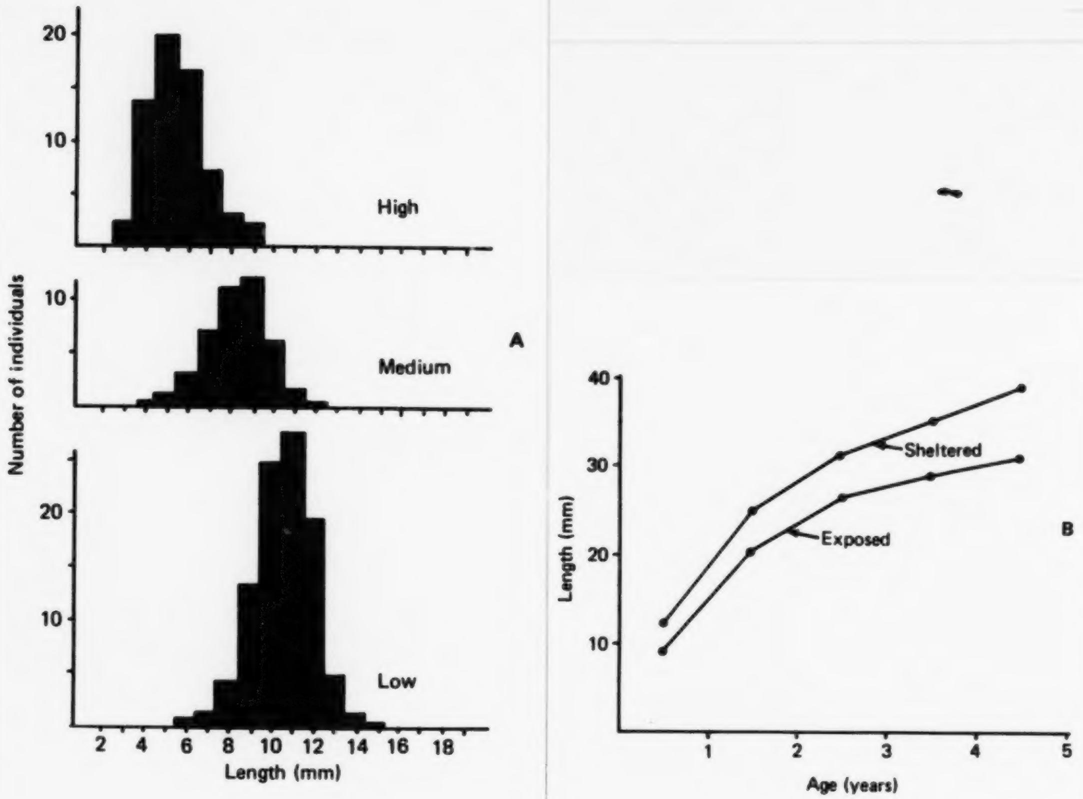

Figure 33. Differences in population attributes along a stress gradient. (a) Size-frequency histogram for the 0+ year-classes of Cardium edule from Llanrhidian Sands, Burry Inlet, South Wales. The stations shown differ in height in relation to low-water level. Average shell lengths reflect rates of growth. Higher stations are more exposed and individuals have a shorter feeding period. After Cole (1956). (b) Average shell growth for two populations of Cardium edule showing effect of exposure to wave action. Both localities are in Essex. Data from Cole (1956).

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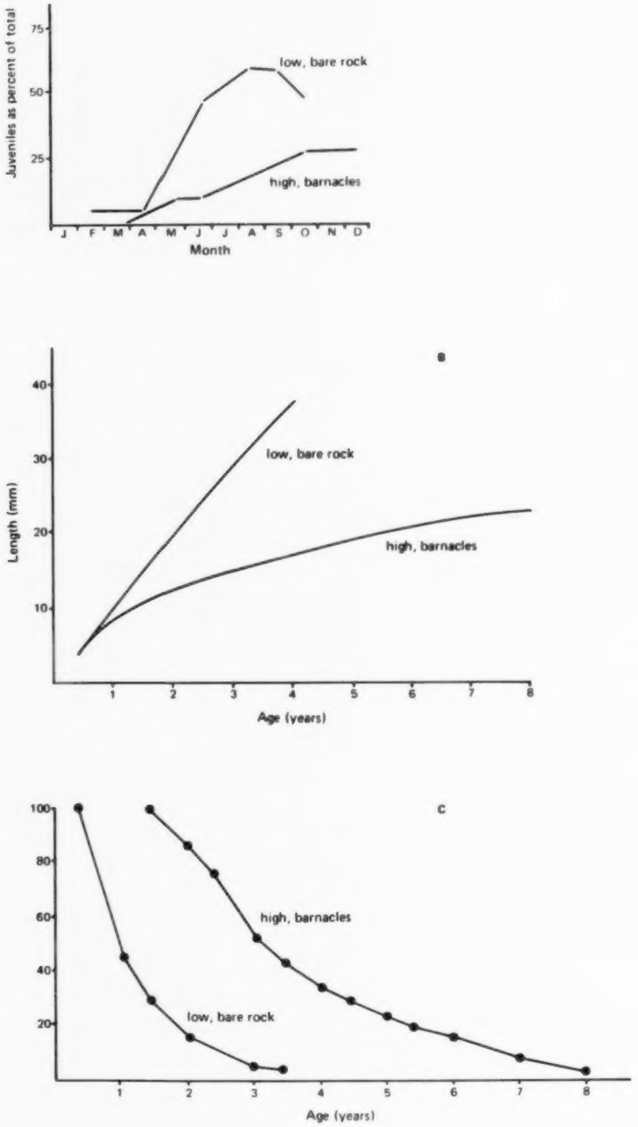

Figure 34. Differences in population attributes in intertidal populations of the limpet Patella vulgata. (a) Recruitment. (b) Growth. (c) Mortality. General trends are illustrated. The population structure at low tidal level on bare rock was markedly influenced by annual recruitment, and showed high rates of growth and mortality. Populations at high tidal level living in barnacle encrusted areas showed lower rates of growth and mortality, and annual spawning represented a smaller percentage of the standing crop. After Lewis and Bowman (1975).

Table 1.

An example of a frequency table.

Length (mm)	Frequency (Number of Individuals)
28 - 30	9
31 - 33	17
34 - 36	32
37 - 39	24
40 - 42	19
43 - 45	6

Table 2. Life table for the California Pismo Clam, Tivela stultorum, recomputed from Hallam (1967). Mortality data from Fitch (1950).

Age (years)	Age as % deviation from mean length of life	Number surviving at beginning of interval out of 1,000 born	Number dying in age interval out of 1,000 born	Mortality rate per thousand alive at beginning of interval	Average number of individuals alive during age interval	Number of individual time units left at beginning of interval	Expectation of life, or mean lifetime remaining to those attaining age intervals (years)
x	x'	l_x	d_x	$1000q_z$	L_x	T_x	e_x
0-1	-100	1,000	550	550	725	1569	1.57
1-2	-36	450	202	449	349	844	1.87
2-3	+27	248	72	290	212	495	1.99
3-4	+91	176	60	341	146	283	1.60
4-5	+155	116	60	517	86	137	1.60
5-6	+219	56	38	678	37	51	1.18
6-7	+282	18	13	722	11.5	14	0.90
7-8	+346	5	5	1,000	2.5	2.5	0.75
							0.50

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Table 3.
Relations for computing the statistical quantities appearing in a life table.

$$x' = 100(x-e_0)/e_0$$

$$d_x = l_x - l_{x+1}$$

$$q_x = d_x/l_x$$

$$L_x = \int_x^{x+1} l_x dx / \int_x^{x+1} dx$$

$$\doteq (l_x + l_{x+1})/2 \quad \text{if the age interval } \Delta x \text{ is small}$$

$$T_x = \int_x^{\infty} l_x dx$$

$$\doteq \sum_{i=x}^{\infty} L_x \Delta x \quad \text{if the age interval } \Delta x \text{ is small}$$

$$e_x = T_x / l_x$$

Table 4.
Some of the Correlates of r- and K-Selection. From Pianka (1970).

Climate	Variable and/or unpredictable: uncertain	Fairly constant and/or precticable; more certain
Mortality	Often catastrophic, nondirected, density independent	More directed, density-dependent
Survivorship	Often Type III (Deevey 1947)	Usually Type I and II (Deevey 1947)
Population size . . .	Variable in time, nonequilibrium; usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecologic vacuums; recolonization each year	Fairly constant in time, equilibrium; at or near carrying capacity of the environment; saturated communities; no recolonization necessary
Intra- and interspecific competition .	Variable, often lax	Usually keen
Relative abundance .	Often does not fit MacArthur's broken stick model (King 1964)	Frequently fits the MacArthur model (King 1964)
Selection favors . .	1. Rapid development 2. High r_{max} 3. Early reproduction 4. Small body size 5. Semelparity: single reproduction	1. Slower development, greater competitive ability 2. Lower resource thresholds 3. Delayed reproduction 4. Larger body size 5. Iteroparity: repeated reproductions
Length of life . . .	Short, usually less than 1 yr.	Longer, usually more than 1 yr.
Leads to	Productivity	Efficiency

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APPENDICES

Anyone interested in doing shell growth research may find the following appendices useful. Much of the practical information about preparation techniques and methods of analysis are scattered throughout a diverse literature. We have attempted to draw some of this information together.

The appendices deal with the "nuts-and-bolts" aspects of preparing acetate peels, fractured sections, and thin-sections of bivalve shells. The range of techniques outlined here can be used to study most molluscan shell structures. Our readers should understand that some of these techniques require skillful preparation. To gain finesse with the techniques requires some initial patience and experience. If problems arise, it is often most efficient to call or write a specialist in order to resolve difficulties.

In some cases, the authors of the various appendices mention specific products or vendors for supplies and instruments. These suppliers and products are listed only as examples and do not represent the sole source nor do the listings represent our individual or collective endorsement of products or suppliers.

APPENDIX 1

PREPARATION OF ACETATE PEELS AND FRACTURED SECTIONS FOR OBSERVATION OF GROWTH PATTERNS WITHIN THE BIVALVE SHELL

by

Michael J. Kennish

Jersey Central Power and Light Company
Madison Avenue at Punch Bowl Road
Morristown, New Jersey 07960

Richard A. Lutz and Donald C. Rhoads

Department of Geology and Geophysics
Yale University
New Haven, Connecticut
06520

ACETATE PEELS

Throughout various chapters of this manual (especially Chapters 2 and 3), reference has been made to acetate peel replicas of polished and etched bivalve shell sections. Such peel replicas are easily and rapidly prepared: seven procedural steps are involved: (1) embedding; (2) sectioning; (3) grinding; (4) polishing; (5) acid-etching; (6) washing and drying; and (7) application of acetone and acetate. We will describe these steps and give examples of specific products various workers have used.

(1) Embedding

As an initial step, individual shell valves are embedded in an epoxy resin to prevent fracturing during sectioning. Rhoads and Pannella (1970) have reported success using Epon 815 resin and DTA curing agent from the Miller Stephenson Chemical Co., Inc., Danbury, Connecticut 06810; a modification of their method follows.

The epoxy solution should be prepared by thoroughly mixing the reagents in a ratio of 1 part DTA curing agent to 10 parts Epon 815. A greater proportion of curing agent should be avoided due to the exothermic reaction of the curing agent-resin mixture. Each pouring of epoxy should be restricted to thicknesses no greater than 2 cm; pouring thicknesses greater than this may result in a violent exothermic reaction. Embedding of large shells, which require greater thicknesses of epoxy, should be accomplished by building up 2 cm-thick layers one at a time. Disposable plastic containers (e.g. PEEL-A-WAY tissue embedding molds, Lipshaw Manufacturing Co., 7446 Central Avenue, Detroit, Michigan 48210) can be used as non-sticking molds for the epoxy. After placing a shell valve in the liquid epoxy mixture, the entire container should be placed under vacuum. After approximately five minutes, the vacuum is released and then the evacuation is repeated for another five minutes. This procedure should be repeated until no air bubbles remain in the epoxy. The mixture may then be left at ambient pressure to cure. Curing time for the mixture is approximately 6-8 hours at room temperature.

(2) Sectioning

After the epoxy has hardened, the embedded shell may be sectioned along the desired axis, using a diamond rock saw (e.g. various models of saws from Buehler Ltd., 2120 Greenwood Street, P.O. Box 830, Evanston, Illinois 60204; solid rim blades with #1 concentration of diamonds from Felker Operations, Dresser Industries, Inc., 1900 South Crenshaw Boulevard, Torrance, California 90509). Because the epoxy is transparent, it is possible to examine the embedded shell and to define a transect for this section; this transect may be scratched directly on the epoxy surface to serve as a guide during sectioning. In the majority of studies of internal bivalve growth patterns, the valve(s) are sectioned along the axis of maximum growth (Fig. 1a-b; see also Chapter 1). This cut is oriented so that growth increments intersect the plane of section at right angles (Fig. 1).

(3) Grinding

Once cut, valve cross-sections are ground sequentially on cast iron lapidary wheels using carborundum powders in the following order of grit sizes: 120; 240; 320; 400; and 600 (e.g. Buehler carborundum grits). If the saw cut is sufficiently smooth, it may not be necessary to use the coarsest grits early in this grinding sequence. Shell surfaces and all lapidary surfaces must be thoroughly cleaned after each grinding step in order to avoid contamination of the successively finer grits by the earlier coarse grits. As an alternative grinding procedure, one may utilize pressure-sensitive grinding discs (e.g. Buehler Ltd.), AB carbimet special silicon carbide wet grinding papers which are mounted on the lapidary wheels. These discs are available with the same size grits as the carborundum powders described above and should be used in the same sequential order (i.e. 120; 240; 320, etc.). If lapidary equipment is not available, grinding may be done directly on glass plates. For the final two grinding steps on glass, one should use 2000, followed by 3000, grade carborundum grits. No polishing (next step) is necessary if the surfaces are finely ground on glass in this manner.

(4) Polishing

After sequential grinding (down to a 600 grade carborundum grit), surfaces are polished with 2000, followed by 3000, alumina powders [e.g. LINDE (Union Carbide, Crystal Products, Electronics Division) alumina powder abrasive] on a high-speed lapidary wheel covered with a polishing cloth (e.g. Buehler Ltd., AB microcloth #40-7208). A separate cloth must be used for each grit and the lapidary wheel must be thoroughly rinsed after each polishing step.

(5) Acid-etching

After polishing, sections are etched by immersing them in a dilute solution of hydrochloric acid [1 part concentrated (38%) HCl to 100 parts distilled H_2O] for periods ranging from a few seconds to a few minutes. Optimal etching time will vary with the species examined and is related to shell structure, mineralogy, organic content, and state of preservation. The acid-etching process is a critical step in the technique and it is recommended that a series of etching times be carried out to determine optimum etching periods for a particular specimen.

(6) Washing and Drying

Immediately after etching the specimen, the acid must be thoroughly rinsed from the sectioned surface. The section should be set aside to air-dry. Drying time can be reduced by spraying acetone on the etched surface.

(7) Application of Acetone and Acetate

The etched shell surface is flooded with acetone, and a piece of sheet acetate (∿ 3 mm thick) is firmly applied to this surface. In order to eliminate air bubbles, one end of the piece of acetate should be placed at the edge of the cross-section and then slowly lowered onto the meniscus of acetone, applying firm pressure. This procedure is similar to placing a cover slip onto a glass slide. A small weight should then be placed on top of the acetate to insure a firm contact of the epoxy block with the acetate. After the acetone has evaporated (20-30 minutes), the peel is removed from the cross-section and, if desired, mounted onto a glass slide with Canada balsam or one of a number of synthetic resins prior to examination under the microscope.

Acetate peel replicas may alternatively be prepared using extremely thin acetate. If this is done, the acetate should be placed on a clean piece of glass. The shell cross-section is then flooded with acetone and firmly applied onto the acetate. Once again, air bubble formation may be minimized by placing one end of the cross-section at the edge of the acetate and slowly lowering it onto the acetate, applying firm pressure throughout this process. A weight should be placed on top of the epoxy block. After 20-30 minutes, the acetate can be removed and should be immediately mounted between two glass slides to avoid curling and wrinkling.

FRACTURED SECTIONS

Fractured sections of bivalve shells are extremely easy to prepare for scanning electron microscopic examination. Shell valves should be thoroughly dried prior to fracturing; placement of the valves in a desiccator is advisable for shells from which soft tissues have recently beem removed. Once dry, the shells may be fractured (i.e. broken) along the desired axis. For fracturing, it is generally advisable to place the shell on the edge of a solid object (e.g. a firm table) with the desired transect superimposed directly over the edge (of the table) itself. Firm pressure may then be applied to the unsupported portion of the shell extending beyond the (table's) edge until the shell breaks. It is important to break the shell away from any shell surface that is of interest (e.g. if one is interested in examining the periostracum of a given shell valve, the shell should be placed on the edge of the object (table), with the periostracum side of the valve up; pressure is then applied downwards so that the break itself is away from the periostracum). After fracturing, the shell fragment may be mounted on a standard SEM stub. Care should be taken to insure electrical conductivity between the specimen and the stub; the use of silver paint or graphite-containing solutions (e.g. DAG 154; Ted Pella, Inc., Cat. No. 1603-16) as mounting media generally adequately provides such conductivity. Clean compressed air should be used to remove all contaminants from the surface of the fractured section. Finally, the specimen should be coated (under vacuum) with gold-palladium or a combination of gold and carbon.

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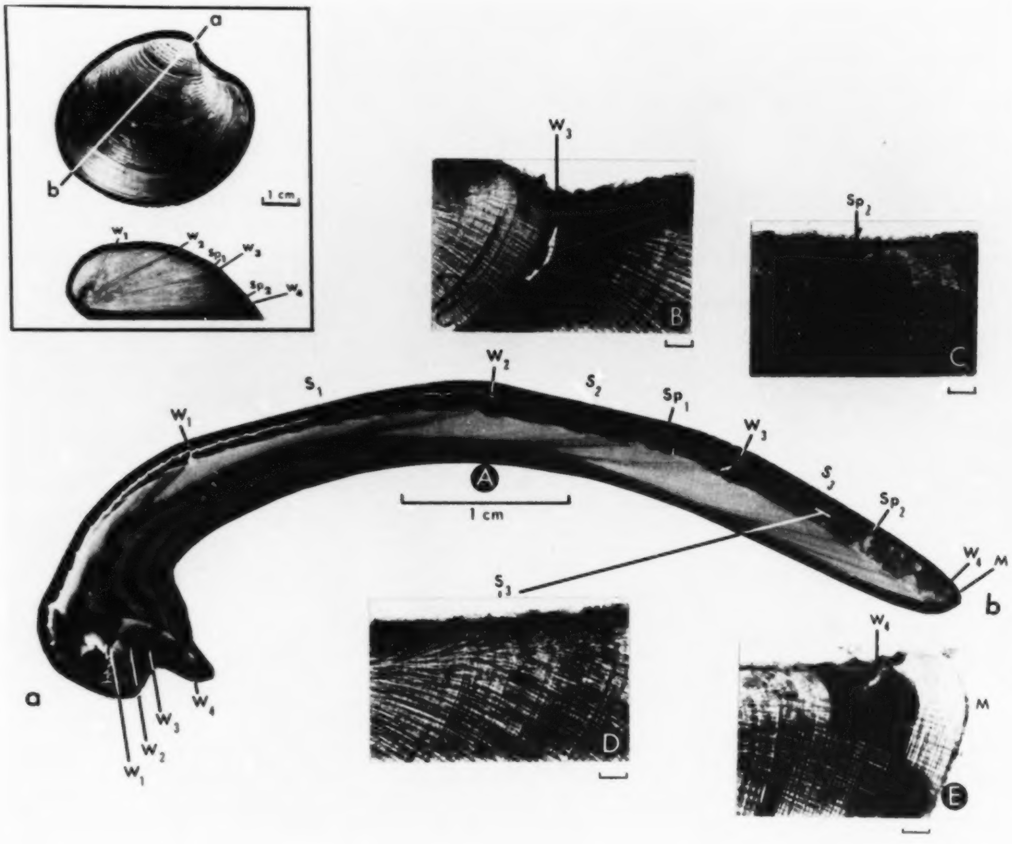

Figure 1. Illustration of bivalve shell sectioning technique. Box inset at upper left depicts axis of maximum growth (a-b) and external shell growth patterns of Mercenaria mercenaria. (A) Polished section along axis of maximum growth (a-b) of a specimen (depicted in inset) collected during the fourth winter (W_4). S_1, S_2, S_3; summer growth. Sp_1, Sp_2; spawning breaks. M; shell margin. (B-E) Microgrowth increments in specific shell regions of (A). The unlabeled scales equal 100 μm.

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APPENDIX 2

THE STUDY OF BIVALVE SHELL STRUCTURE AND GROWTH LINES USING THIN-SECTIONS

by

George R. Clark II

Department of Geology
Kansas State University
Manhattan, Kansas
66506

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THIN-SECTIONS

Early studies of molluscan shell structure, culminating in the classic work of Bøggild (1930), were based upon examination of petrographic thin-sections of shells. The grinding of such sections required a considerable investment of time and labor, and, because of the tendency of many shells to split along growth surfaces of crystal boundaries, modern high-speed thin-sectioning equipment has not appreciably lessened this problem.

For this reason, acetate peels (see earlier section of this Appendix) have largely replaced thin-sections in recent research on shell structure and growth lines. Although they provide much less information than thin-sections, acetate peels can be prepared in a fraction of the time with little training.

New equipment, however, may again reverse the trend. The introduction of low speed diamond saws, such as Buehler's Isomet 11-1180, makes it possible to prepare high quality thin-sections nearly as easily as acetate peels.

Micrographs in Plate I, which are all from a recent report on seasonal growth variations in *Mercenaria* (Clark 1979; see also Clark 1977), illustrate the type of information available in thin-sections at relatively low magnifications. In addition to those features visible on acetate peels, these sections show variations in transparency, pigmentation, and crystallographic orientation. Higher magnification studies can make use of the finite thickness of the thin-section to make limited observations in three dimensions. Thin-sections are also much easier than peels to store and study, having no surface relief to protect and no tendency to curl up. As thin-sections can now be prepared with little more effort than peels, they should become a useful supplement if not a replacement.

The first step, as in making a peel, is to cut the shell along the desired plane of section. This can be accomplished with no preliminary embedding on a low speed saw. When the cut is completed, the sectioned surface is lightly sanded or ground using 600 or 1000 grit. Some care should be taken to insure that only a single planar surface is present after this operation, as it is easy to develop two facets by a back-and-forth grinding motion. This surface should be thoroughly cleaned to remove grit, cutting oils, or other contaminants; ultrasonic cleaning may help if the shell is not too delicate.

After drying, the sectioned surface must be cemented to a petrographic slide. I find the bonds are improved when the slides are "frosted" beforehand with 600 grit. Both the section and the slide must be dry and free from oils or fingerprints. A variety of cements may be used, but thermoplastic cements such as Lakeside and high temperature epoxies such as "Petropoxy" will often fail due to thermal stress on cooling. I find Ward's "Bioplastic", which cures at 70°C, satisfactory for most purposes. Only a few drops of cement should be used, for a large buildup of excess cement at the base of the section will prolong the cutting time and may warp the saw blade.

When the bond between section and slide is well developed, the slide should be mounted parallel to the saw blade and a second cut made about 200 μm (.008 inch) from the surface of the slide. The section should be lowered carefully onto the blade to make sure the blade is not deflected by the cement.

Upon completion of the second cut, the slide can be ground by hand on a glass plate with 600 or 1000 grit in less than ten minutes. The goal here is transparency, not a specific thickness, so progress can be readily judged and a tendency to grind too fast on one side can be compensated for before it is too late.

After cleaning, the thin-section can have a cover slip permanently attached with Canada balsam or epoxy, or can be studied with a temporary cover slip using immersion oil as a bond. The latter method permits staining or additional grinding at a later time.

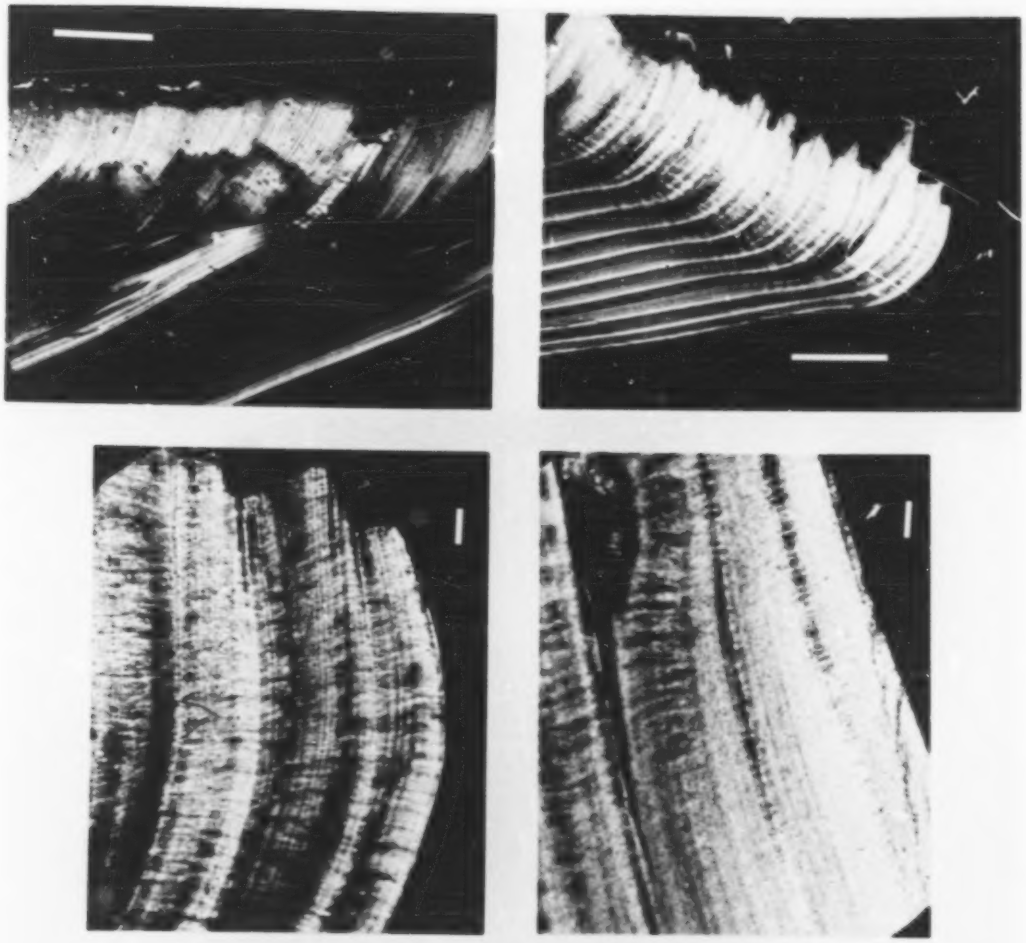

Plate 1. (a, b, c & d) (A). Thin-section of mature region of a specimen of Mercenaria mercenaria. Scale bar equals 1 mm. (B). Thin-section of margin and senile region of a specimen of Mercenaria mercenaria. Rectangle indicates position of micrograph (C). (C). Thin-section of the margin and outer shell layer of the senile region of a specimen of Mercenaria mercenaria. Scale bar equals 0.1 mm. (D). Thin-section of the middle shell layer and inner surface in the senile region of a specimen of Mercenaria mercenaria. Scale bar equals 0.1 mm. (E). Thin-section of the outer shell layer of mature region of a specimen of Mercenaria mercenaria. Scale bar equals 0.1 mm. All micrographs from Clark (1979).

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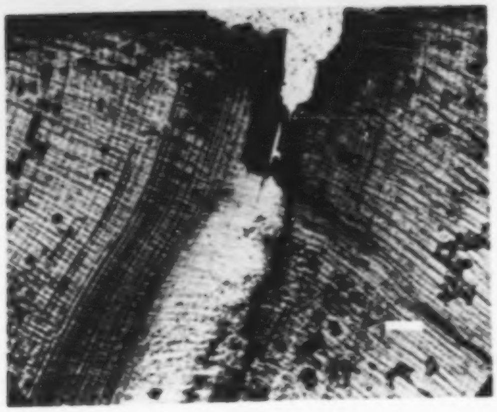

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Plate 1(e)

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APPENDIX 3

TECHNIQUES FOR OBSERVING THE ORGANIC MATRIX OF BIVALVE SHELLS

by

George R. Clark II

Department of Geology
Kansas State University
Manhattan, Kansas
66506

Although mollusc shells are built primarily of various structural arrangements of calcite and aragonite, these minerals are invariably accompanied by organic constituents. Some of the organic matter forms obvious functional structures such as the ligament and the periostracum, but much of it is distributed throughout the shell as the organic matrix.

The organic matrix appears to be an essential participant in the calcification process, and for this reason has attracted the attention of many investigators [see literature summaries in Wilbur (1972, 1976), for example]. Most of the older work is directed toward questions of composition and ultrastructure of the matrix, but an increasing amount of attention is being paid to the morphological relationships between the organic matrix and carbonate crystals. Numerous workers (Bevelander and Nakahara 1969; Erben 1972, 1974; Erben and Watabe 1974; Mutivei 1970, 1972a, 1972b; Taylor and Kennedy 1969; Towe 1972; Towe and Hamilton 1968; Towe and Thompson 1972; Travis 1968; Wada 1961, 1972; Watabe 1963, 1965; Wise 1970; Wise and Hay 1968) have noted that the most prominent organic matrix forms sheets which separate layers of crystals (interlamellar matrix) or isolate individual crystals (intercrystalline matrix). The precise physical relationships are of considerable interest, for it appears that the nucleation of individual crystals takes place on the organic surfaces and that these influence the mineralogy and crystallographic orientation of the crystals. This "template" hypothesis has received wide acceptance, but a further interpretation of the matrix-crystal relationship, by which the sheets of matrix are thought to confine and eventually terminate the growth of individual crystals (the "compartment" hypothesis), is the subject of considerable controversy (Bevelander and Nakahara 1969; Erben 1972, 1974; Lutz and Rhoads 1977; Mutvei 1970, 1972; Towe 1972; Towe and Hamilton 1968; Wada 1972).

Our understanding of the organic matrix has been limited by difficulties in preparation. Light microscopy of thin-sections cannot reach the magnification required to distinguish most matrix elements, and scanning electron microscopy cannot readily discriminate between organic and crystalline elements in fractured or polished sections. Decalcification can eliminate the crystalline elements, but the matrix is then prone to collapse or shrink when dried. Transmission electron microscopy can make such distinctions, but the preparation of ultrathin-sections showing undistorted relationships between matrix and crystals is extremely difficult, and even when achieved will only exhibit two dimensions of a complex three-dimensional structure.

I have found that the application of critical point drying to oriented sections which have been polished and then very slightly etched results in organic matrix preparations highly suitable for scanning electron microscopy (Clark 1978). Limiting the decalcification to a depth of only a few micrometers insures that the exposed organic matrix will maintain dimensional stability and retain its proper orientation with respect to the dissolved portions of the carbonate crystals. Using critical point drying eliminates the crushing effect of surface tension experienced during drying in air. Polishing the sectioned surface before etching is necessary to ensure that the very thin zone of matrix exposed by etching is free from damage (scratches) and mechanical distortion. This also serves as a check on the success of the final preparation, for if no distortion has occurred during etching or drying, the exposed matrix should appear truncated along a planar surface.

Plate IA-C illustrates the basic advantages of this technique as applied to an examination of the organic matrix relationships between the pallial myostracum (center band) and the nacreous layer in a specimen of Mytilus californianus. The organic matrix is present in the fractured section (Plate IA), but cannot be readily distinguished. In Plate IB the organic matrix has been collapsed onto the etched surface in an air-dried preparation. Plate IC, prepared by critical point drying after etching, shows the organic matrix clearly, apparently undistorted. Note that this section, unlike the fractured section, could be made at any angle to these crystals. Other organic matrices prepared in this manner are shown in Plate ID-G. The use of stereo pairs (Plate IE, F) permits the direct visualization of three-dimensional structures.

In addition to improving studies of the organic matrix itself, preparations of this type should be useful in more general investigations. Studies of molluscan shell structure, for example, have long been hampered by the small size and complexity of many arrangements of crystals, and a variety of distinct structures classified as "complex" or "homogeneous" since the classic work of Bøggild (1930) remain to be adequately described. Stereo pairs of the matrix (Plate IE, F) can be used to determine the physical orientation of crystals and crystallites. Also, because matrix preparations can be oriented in any direction and, in a sense look into the shell, they should provide information not available from fractured or standard (air-dried) etched sections.

Studies on growth lines, particularly those involving variations in shell structure with stress (Kennish and Olsson 1975; Clark 1973) and variations in the accumulation of organic matter (Lutz and Rhoads 1977), can also make good use of this sort of preparation. Various shell structures can be readily interpreted (Plate ID-G) and accumulations of organic matter along growth lines (Plate IG) are very prominent.

Although the details of my method of preparation are of much less importance than the principles, I list them here. Sections of mollusc shells are cut at desired orientations using a low speed diamond saw (e.g. Buehler Isomet 11-1180) to minimize stress and fracture. The sections are embedded in epoxy to facilitate the polishing operations, ground on a glass plate with 600 grit until flat, and then polished with a series of alumina compounds to a final polish with 0.05 μm alumina. After washing with distilled water, the sections are etched for 15 to 30 seconds in 0.1 N HCl, and then, keeping a miniscus of liquid on the specimen surface during every transfer, passed through a series of alcohols until it is in 100% ethanol. The specimens are then dried in CO_2 using a critical point drying apparatus; some care is required to devise holders which protect the etched surfaces during this process, as some turbulence is involved. Finally, the specimens are coated with a combination of carbon and gold-palladium to a total thickness of about 200 A. Micrographs presented in this appendix were taken using an Autoscan scanning electron microscope.

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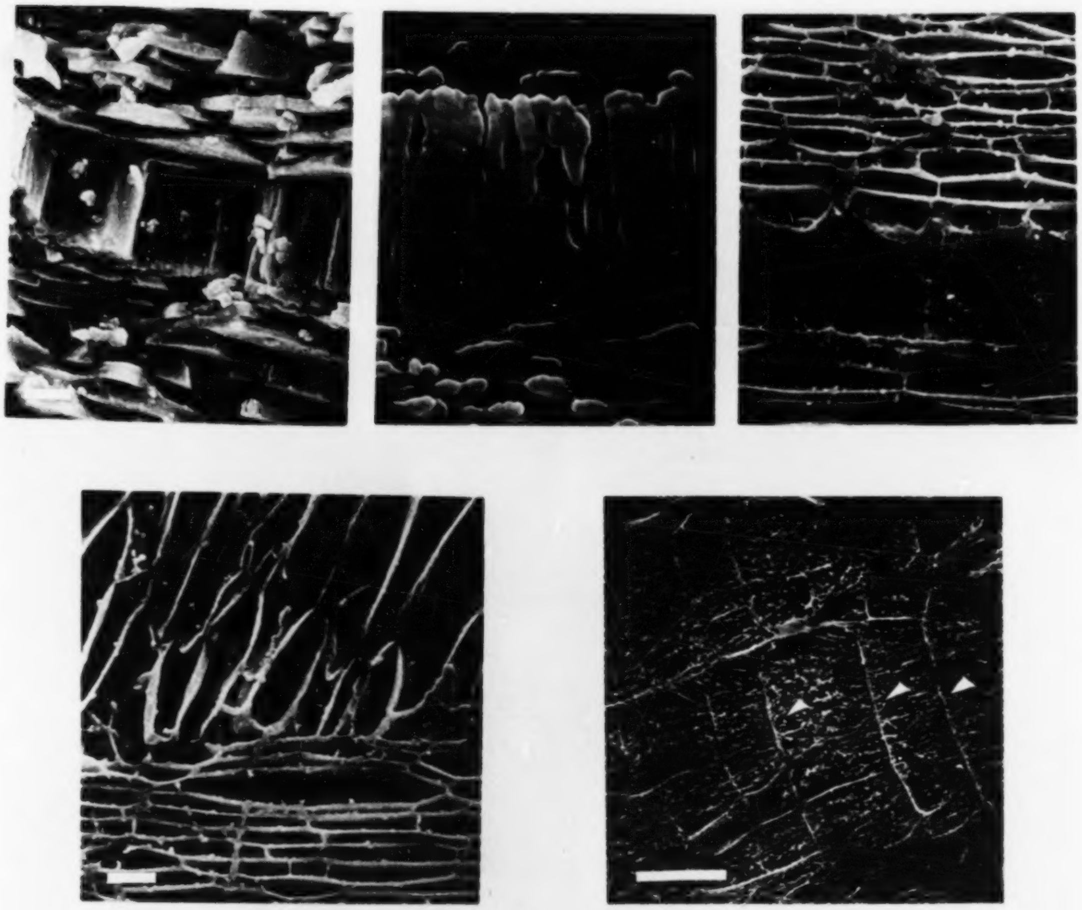

Plate I. (a,b,c, d & e) (A-C). Pallial myostratum (thick layer in middle of micrographs) and surrounding nacreous layers in Mytilus californianus. (A). Fractured section; the organic matrix is present but cannot be readily distinguished from the aragonite crystals. (B). Polished and etched section dried in air. The organic matrix exposed by etching has collapsed over the etched surface. (C). Polished and etched section prepared by critical point drying. The organic matrix stands in high relief above the etched surface. Scale bar for micrographs A-C is depicted in (A) and equals 1 µm. (E, F). Transition zone between outer prismatic layer and middle homogeneous layer in Mercenaria mercenaria. Stereo viewing shows this to be a variety of complex crossed lamellar structure. Scale bar equals 10 µm. (D). Transition from prismatic layer (top) to nacreous layer (bottom) in Mytilus californianus. Scale bar equals 1 µm. (G). Prismatic layer of Mercenaria mercenaria showing prominent growth lines (arrows) formed by concentration of organic matter. Scale bar equals 10 µm.

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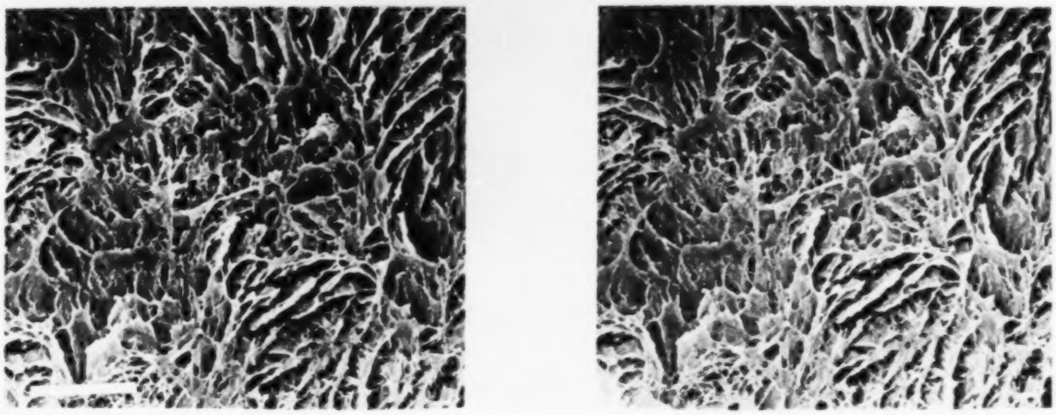

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Plate I (f & g)

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